Title
Extensible tools for movement ecology with applications for the study and conservation of Namibian ungulates

Author
Seidel, Dana Paige

Publication Date
2019

Peer reviewed|Thesis/dissertation

Extensible tools for movement ecology with applications for the study and conservation of Namibian ungulates

by

Dana Paige Seidel

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Wayne Getz, Chair
Professor Michael Boots
Professor Justin Brashares

Summer 2019

Extensible tools for movement ecology with applications for the study and conservation of Namibian ungulates

Dana Paige Seidel

Abstract

Extensible tools for movement ecology with applications for the study and conservation of Namibian ungulates

by

Dana Paige Seidel

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Wayne Getz, Chair

Movement ecology is a young sub-discipline in ecology in which researchers apply high resolution location and activity data to analyze animal behavior across multiple scales: from individual foraging decisions to population-level space-use patterns. These analyses contribute to various other subfields within ecology—*inter alia* behavioral, disease, landscape, resource, and wildlife—and may also facilitate novel exploration in fields ranging from conservation planning to public health.

Using a decade of GPS relocation data from zebra (*Equus quagga*), black rhino (*Diceros bicornis*), and African elephant (*Loxodonta africana*) captured and collared in Etosha National Park from 2008-2018, this dissertation reviews developing methods within movement ecology, extends and applies these methods to a threatened and understudied species, and presents a new software package distilling a growing movement ecology tool set for researchers and managers unfamiliar with the domain specific analyses and/or the command line interface of modern statistical analysis (e.g. `R`).

Despite the growing availability of animal movement data and the potential for broad application in geographic analysis beyond animal ecology, the analytical methods of movement ecology have yet to be fully incorporated in a broader understanding of geographic analysis. Chapter 2, a review written for the Geographical Information Sciences (GIS) community, provides an overview of the most common movement metrics and methods of analysis employed by animal ecologists and emphasizes the potential for movement analyses to promote transdisciplinary research: comparing advances in the young field of movement ecology to

parallel developments within the broader field of geographic information sciences.

Two limitations remain common within the growing field of movement analysis. First, within movement ecology, many, even most, analyses require clean, complete, and regular time series of relocations, limiting the available research on species that are hard to track and/or often return gappy, irregular data; including some of the world's most endangered animals, e.g. black rhinos. In chapter 3, extending and applying recursion analyses to irregular spatio-temporal data from this understudied and critically endangered species, I investigated daily, biweekly and annual recursion behaviors of rhinos, to aid conservation applications and increase our fundamental knowledge about these important ecosystem engineers. Results indicate that rhinos may frequently stay within the same area of their home ranges for days at a time, and possibly return to the same general area days in a row especially during morning foraging bouts. Initial results indicate that recursion at the daily and biweekly scales may be driven by hydration and productivity cycles respectively. Recursion across larger time scales is also evident and likely a contributing mechanism for maintaining open landscapes and browsing lawns of the savanna.

A second, and equally challenging, limitation to the growing movement ecology tool kit is accessibility. The growth in analysis techniques, and the concomitant growth of open-source software for analysis, pose a stumbling block to general acceptance in interdisciplinary and management settings, where researchers may be unfamiliar with the expansive set of tools or the command line interface of modern analysis packages. In chapter 4, to reduce this friction and enhance the accessibility of exploratory data analysis tools for animal movement data, I built `stmove`, an R package designed to make report building and exploratory data analysis simple for users who may not be familiar with the extent of available analytical tools. Furthermore, `stmove` sets forth a framework of best practice analyses, which offers a common starting point for the interpretation of terrestrial movement data, promoting comparability of results across movement ecology studies.

The datasets, analyses, and tools presented in this dissertation seek to enhance communication, application, and accessibility of a growing movement ecology toolkit while providing a special glimpse into a diverse ecological community and the individual and population movement behavior through within Etosha National Park over the last decade. We demonstrate new tools built for exploratory data analysis in movement ecology using this data and explore how insights from movement ecology can help inform successful conservation efforts in the region and beyond.

To Mom and Dad: Thank you.
To little Owen and Lucas: You are so loved, the world is yours.

Contents

List of Figures

List of Tables

Acknowledgments

First I must thank my advisor, Wayne Getz, and the committee members whose support and counsel got me here, Justin Brashares and Mike Boots. I took, perhaps, a unique path to completion and I heartfully thank Wayne for his patience and support along the way. I would also like to thank Perry deValpine and Ian Wang for their participation on my qualifying exam committee, especially Perry for I learned a great deal taking and teaching his statistical courses in the department. Finally, I would like to thank the DS421 program and Carl Boettiger who played a crucial role in my identifying and exercising skills that could serve me beyond academia. Teaching with Carl was one of the most formative and happiest times of my PhD and I am so thankful to have had the chance.

I am grateful to U.C. Berkeley and to the Environmental Science, Policy, and Management department, in particular, for providing the opportunity to pursue my research interests. Thank you to Roxanne and Bianca and the other staff members who help all of us graduate students navigate the Ph.D. world at Berkeley.

Thank you to all my family and friends. Thank you to Eric Dougherty, my very best co-author and travel companion. Thank you to the strong, brilliant women in my life that showed me the way and walked alongside me: Mom, Laura, Ally, Lilia, Fraser, Michelle, Amanda, Jess, Sara, Brittany, and so many more. Although many of us live far apart, you all are pillars in the support system that made this possible. Thank you to my brother Eric for assuring me I had marketable skills even when I didn't see them, and to my Dad for reminding me that didn't mean I needed to listen to my brother when he encouraged me to quit. Thank you to both my parents for always believing in me, for working so hard so we could all have so much, and for being unwaveringly proud; for always being a safety net - both emotional and financial – and for all the free laundry and meals that fuelled this dissertation.

Finally, thank you to Owen. For loving me during the most stressful year of my life and for always striving to make that life a little bit easier. Building a home together became the prize at the end of this long road and I'm so excited to begin new adventures with you.

Chapter 1

Introduction: Tools in Movement Ecology, a new paradigm

Background

The miniaturisation of animal tracking devices and satellite-to-ground communications developed during the late-twentieth century allowed for the study of movement in ways not before possible [93, 50]. Ecology can now be studied as a consequence of, and influence on, movement both on a grander scale than before but also with greater resolution. Researcher now seek to understand ecological patterns through the study of movement as a process, or, alternatively, to understand processes in ecology, like foraging and breeding, as a consequence of movement patterns. From out of this paradigmatic shift, the sub-discipline of movement ecology emerged offering new clarity and dimension to concepts central to animal, especially large animal, ecology for a long time, such as migration, dispersal, home range and territoriality, to name a few; even more importantly, this discipline introduced concepts not previously considered or studied, e.g. recursion or behavioral state analysis.

In general, the field of movement ecology seeks to answer questions regarding where, how, and why individual animals move, placed within the context of diverse natural environments. Movement ecologists consider movement the outcome of behavioral decisions influenced by animals' internal states (e.g. physiological needs), external biological factors (e.g. competition) and their physical environment [126]. Given the importance of this interplay, it is the movement pathway of an individual or group of individuals that is often the central feature studied in movement ecology. Using high resolution tracking data to estimate an animal's continuous path allows researchers to understand what various environmental elements animals are exposed to that may positively or negatively impact long-term processes like reproduction and survival [56]. Using available relocation data and associated datasets, like accelerometery or satellite imagery, researchers can extract and model behavioral modes and decisions, test hypotheses regarding predictors of animal movement and attempt to explain

how individual behavior scales up to the landscape-level distribution of animal populations that are often the focus of conservation concern or ecosystem management policy.

The study system

Within the chapters of this dissertation, I review, apply, and extend the movement metrics available to researchers today using unique datasets from Etosha National Park's remarkable ungulate populations. Etosha National Park is an approximately 23000 km^2 national reserve and park in northern Namibia. It is a semiarid savanna with a natural east-west rainfall gradient of 450-200 mm/yr [199]. The park supports a high density of ungulate species including zebra (*Equus quagga*), springbok (*Antidorcas marsupialis*), elephant (*Loxodonta africana*), and rhino (*Diceros bicornis*). Within the bounds of the park, there is an estimated population of 13,000 zebra, 15,600 springbok, and 2,600 elephant [173, 171, 44]. Etosha National Park and conservations lands to the east and south of the park, support some of the last remaining free-ranging populations of black rhino. While populations roam the length of the park, a higher density of individuals were tracked in the eastern region. A large pan lies in the interior of the park, uninhabitated by most individuals but bordered by highly trafficked waterholes and animal corridors; beyond the pan, the landscape is topographically featureless [139]. Etosha has been fully fenced since the early 1970s, though, from tracking, it is apparent some individuals do occasionally cross the fences. Artificial waterholes provide water year round throughout the park [171].

Methods & metrics for GPS relocation data

While the seminal paper on the new "movement ecology paradigm" is only a decade young [126], telemetry data, and emerging methods and metrics to analyse them, have been around for more than half a century. Indeed, the broader field of geographic information science has been developing for just as long (the term was coined in 1968) and spatial analysis of process and pattern much longer (see examples of epidemiological mapping as early as the 19th century) [37]. Within the field of movement ecology, multiple recent reviews have been written that explore the development of individual analyses or metrics of space use (e.g., home ranges [43], proximity/social networks [136], selection functions [102]). However, few have attempted to outline the complete scope of metrics and tools used to analyze animal movement data and none have explicitly identified movement ecology's place within the larger realm of geospatial analysis and its connections to the geographic information science (GIS) community. While it is clear there is interest within the GIS community in applications of movement analysis for spatial ecology [155, 96, 98, 97, 108], generally in the field, quantitative analysis of movement takes a broader view, acknowledging the potential for similar metrics to analyse movement of a variety of applications including a growing interest in human mobility [50, 109, 33]. Indeed, questions relating to geospatial data analyses that address the behavior of individuals, the demography of populations, and the structure of landscapes in the face of global change are of interest to geographers and movement ecologists alike and the potential

for trans- and inter-disciplinary research great. To better facilitate communication and research between these fields, Chapter 2 provides a broad exposition of metrics and methods of analysis that are widely used in the movement ecology field, emphasizing their applications beyond animal ecology into more general geospatial analysis. Throughout, similar metrics already adopted or developed by researchers in GIScience and the advances made in the field of movement research more broadly are highlighted. By identifying highlighting the overlap between the two fields, Chapter 2 hopes to provide ecologists and geographers new perspective on the tools available for movement analysis.

Extending movement tools for irregular data

A common requirement of many, perhaps even most, methods for spatio-temporal analysis, across all fields, is a regular time series of data points, i.e. data sampled at consistent, equal-sized, intervals. Analyzing irregular time series, i.e. data sampled at inconsistent intervals, often requires downsampling, timestamp rounding, or various methods of interpolation to achieve regular intervals. In the context of wildlife research, and particularly when trying to identify or model animal behavior, these methods which often lead either to significant data loss or high rates of interpolation, may bias or limit accuracy of results and the strength of conclusions. The nature of animal movement, however, means tracking data is especially prone to GPS error, missed fixes, satellite blocking, etc.. For example, animals may move into forests to rest or forage, dive underwater, or wade in mud – all natural behaviors that can have a nonrandom impact on error rates of telemetry. In the context of wildlife research, state space models have recently become popular as a way to model the movement process even in the presence of irregular data [133, 90, 108], however these hierarchical models however can be challenging to fit and validate. Overall, a lack of simple metrics for gappy, irregular, or error prone datasets, no doubt limits the behavioral and ecological analyses including these species. Furthermore, given the increasing ease of collecting GPS data but the relative challenge of analysing it, there is likely a lot of GPS data going unanalyzed because of the challenges and limitations of fine scale analysis methods for irregular spatial time series data.

In a novel extension of recursion analysis, Chapter 3 addresses this issue using a never before published dataset of relocations from 59 black rhino, a critically endangered and understudied species (with respect to their meso-scale movement patterns). Recursion analyses, broadly referring to methods for detecting returns to prior locations over the course of a movement trajectory, allow researchers to ask questions about the distribution of important resources within an individual's range and can increase our understanding of factors governing movement dynamics [11, 18]. Furthermore, in the context of conservation planning and range management across a fractured metapopulation of reserves, identifying habitats or corridors with high recursion may have even greater importance. By extending recursion analysis to look at daily movement patterns and applying analogous analyses at biweekly, and annual scales as well, I was able to evaluate behavioral questions even confronted with

irregular data. Applying recursion analyses over multiples scales can offer new insight into old assumptions about rhino movement behavior, may help us better understand the mechanisms by which they engineer their environment, and how best to conserve these free ranging populations across a fragmented reserve system.

Democratizing movement data analysis

Many, if not all, of the metrics I discuss in the first two chapters can be applied using modern statistical programming languages like R, Matlab, or Python. Indeed, with the expansion of metrics for movement analysis there has been a concomitant expansion of software to help implement analyses. (The supplementary material to chapter 2 cites many such software packages.) In fact, a recent review found 57 individual R packages solely dedicated to movement or tracking analyses; critically, however, only 12 of these had good to excellent documentation [92]. The proliferation of these tools is both a gift and a stumbling block. For those fluent in a programming language or languages, as more and more young scientists are, this software can expedite the analysis process and expand the possibilities of research questions asked and answered. However, open-source software, especially that which is developed by scientists rather than fluent programmers, comes with no guarantee, often limited consistency and compatibility with other programs, and regularly, as noted above, without the documentation necessary for effective communication and understanding of the functionality contained. What's more, for managers and researchers without this experience, accessibility to this expanding tool set is limited and the sheer number of analyses and packages available to learn can compound the problem.

The movement ecology paradigm [126], which effectively situated the emerging discipline within the broader ecological context, fell short of dictating a set of baseline analyses that should be run on movement data. The absence of a core set of standardized analyses among the many novel tools available to researchers has made it difficult to contextualize the movement patterns of an animal or species and to compare across studies and wildlife. Chapter 4 presents a new R package, `stmove`, designed specifically to address these issues. `stmove` is designed to standardize exploratory data analysis for GPS relocation data by curating a specific set of analyses necessary for exploring movement data. The primary advantage and goal of this package is to provide a simple, single-command procedure to produce comprehensible and customized reports covering important baseline analyses one should conduct on GPS movement data. By bringing together these analyses into one package, addressing compatibility issues, and carefully documenting each function, `stmove` tries to reduce the accessibility challenge faced by researchers and managers unfamiliar with command line programming or the breadth of available movement analyses.

In concert, the following three chapters serve to highlight and advance new methods and metrics in the young field of movement ecology, emphasizing communication and accessibility across disciplines, data, and applications.

Chapter 2

Ecological metrics and methods for GPS movement data

Dana Paige Seidel Eric R. Dougherty Colin J. Carlson Wayne M. Getz

Originally published in *International Journal of Geographic Information Sciences* (2018; **5**:19) and reproduced here with the permission of Eric R. Dougherty, Colin J. Carlson, and Wayne M. Getz.

2.1 Abstract

The growing field of movement ecology uses high resolution movement data to analyze animal behavior across multiple scales: from individual foraging decisions to population-level space-use patterns. These analyses contribute to various subfields of ecology—*inter alia* behavioral, disease, landscape, resource, and wildlife—and facilitate facilitate novel exploration in fields ranging from conservation planning to public health. Despite the growing availability and general accessibility of animal movement data, much potential remains for the analytical methods of movement ecology to be incorporated in all types of geographic analyses. This review provides for the Geographical Information Sciences (GIS) community an overview of the most common movement metrics and methods of analysis employed by animal ecologists. Through illustrative applications, we emphasize the potential for movement analyses to promote transdisciplinary GIS/wildlife-ecology research.

2.2 Introduction

The study of movement as a sub-discipline within the geographic information sciences is developing rapidly, driven by advances in localization technologies used to collect movement data [50, 196]. Parallel to this expansion is the emergence of the field of movement ecology, which seeks to answer questions regarding where, how, and why individual animals move, placed within the context

of diverse and varying natural environments [126]. In movement ecology, the movement pathway of an individual (or a group of individuals) is often the central feature studied. These pathways, considered within the heterogeneous landscapes they cross, expose individuals to various environmental elements that may positively or negatively impact long-term processes like reproduction and survival [56]. For example, an individual's movement decisions, moving them toward or away from a resource-rich area, will directly impact their foraging success and, hence, fitness [73, 74]. At a broader scale, emergent spatial processes and patterns (e.g. the distribution of resources, disease transmission, and human-wildlife conflict) are all influenced by the movement decisions of animals. In this sub-field of ecology, the rapid technological advances driving data collection are facilitated by a conceptual framework for considering animal movements (Nathan's movement ecology paradigm [126]) and catalyzed by the development of new metrics and analytical tools.

Where movement ecology has a limited focus and specific ecological applications, research within the GIScience community into the quantitative analysis of movement takes a broader view, and in many cases has developed or adapted similarly powerful methods for the exploration of movement, both with and without specific ecological application. In movement ecology, multiple recent reviews have been written that explore the development of individual analyses or metrics of space use (e.g., home ranges, proximity/social networks, selection functions; see [43, 136, 102], respectively). In the same period, several special issues in the GIS community have been published on the topic of quantitative movement analysis and spatial ecology [155, 96, 98, 97, 50]. Despite these domain-specific reviews and broader special issues, an exposition that provides an broad overview of metrics and tools used to analyze animal movement data is still needed. Our intention here is to provide such an exposition by reviewing metrics and methods of analysis that are widely used in the movement ecology field, emphasizing their applications beyond animal ecology into more general geospatial analysis. Throughout, we attempt to highlight similar metrics already adopted or developed by researchers in GISscience and the advances made in the field of movement research more broadly. For the most part, our review will emphasize methods most useful for analyzing high-resolution (also referred to as fine-scale) spatio-temporal location data from GPS tags (on collars, harnesses, or secured by other means), often paired with data from accelerometer, proximity, and physiological (e.g., temperature) sensors. While we acknowledge the significant contribution of additional localization technologies (e.g. acoustic arrays, light-based geolocators, VHF/radio data, ARGOS, and the upcoming ICARUS initiative [135]) to the recent expansion of movement research, the metrics developed for these pipelines are, for the most part, outside the scope of this review.

We begin our exposition by organizing movement ecology metrics according to whether they summarize one- (i.e. having only the dimension of length) or two-dimensional (i.e. having the dimensions of area) objects. This approach reflects Smouse's 2010 [157] dichotomy of statistical analyses of relocation data in terms of Lagrangian methods focusing on discrete-step, time-interval, and turning-angle constructs (i.e., a one-dimensional view of movement pathways) and Eulerian methods focusing on emergent space-use constructs (i.e. a two-dimensional view of movement pathways). Within this dichotomy, we distinguish metrics by whether or not they have an environmental covariate context and whether they pertain to individuals or groups of individuals. The methods we discuss represent the range of questions movement ecologists generally address, from inferring animal behavior to understanding the structure and characteristics of the landscape. The first set

of metrics is associated with one-dimensional objects: those metrics intended to derive descriptive statistics from individual movement trajectories and to investigate individual behavioral states across a trajectory. The second set are applied to two-dimensional objects: those meant to describe the frequency with which an individual or multiple individuals occur in a given area or to predict spatial usage patterns for an entire population of a particular species, rather than a single individual. These latter analyses inform researchers about the relationship between landscape structure and animal behavior. Throughout the review, we use data from a single zebra to demonstrate reproducible examples of selected metrics across scales. See Zidon et al. [199] for details on the zebra population from which these data were collected and supplementary information for specific details on individual AG256, the zebra data used here.

2.3 Trajectory Analyses

The improvement of modern tracking devices has led to a considerable increase in the amount of movement data available for analysis, specifically in the form of lengthy time-series of discrete relocations in two or three dimensional space [168]. The level of correspondence between these relocations and the actual movement of the animal will vary, depending on the spatial and temporal resolution of the trajectory, but several metrics can be derived from the path to describe the general, usually statistical, tendencies of individual animals (Table 2.1).

Path-level analyses

Path-level analyses rely on several straightforward metrics that can be easily extracted from consecutive relocations in a time series of geographical points. These metrics are broadly referred to to as stepwise characteristics and can be split into primary and secondary metrics. Primary metrics, such as *step length* and *turning angle* (Table 2.1) are directly derived from relocations at each time step. However, they are highly sensitive to the spatial and temporal resolution at which the data were collected [36, 68]. Secondary metrics may be summary statistics derived from primary metrics [56] or they may be computed from the trajectory at coarser spatio-temporal scales than represented by the raw data. These coarser scale metrics include *net squared displacement* (NSD) [26], which under a pure diffusive movement process scales linearly with time [21], and *residence time* (Table 2.1). They may used, as in the case of NSD, to characterize the functional mode of a movement path (i.e., migratory vs. territorial; [13]). The coarser-scale at which they are calculated makes them less sensitive to the spatio-temporal resolution of the data, provided the scale of the raw data is sufficiently fine (i.e., an order of magnitude finer than these secondary measures).

Metrics have been developed to describe structural aspects of movement trajectories that include many twists and turns. Two of these are the *straightness index* and *tortuosity*: both measure the degree to which movement trajectories deviate from straight lines (Table 2.1). A third is a trajectory's *fractal dimension*: informally, it has a value between one and two, and is a measure of the extent to which a one-dimensional trajectory fills two-dimensional space, as an individual meanders around the landscape (values close to 2 represent trajectories that are more "space filling" than those with dimensions close to 1). These three structure-characterizing metrics are calculated across a series of steps (i.e. consecutive locations in space), typically using computer algorithms,

although the fractal dimensions of earthworms moving in vegetated versus unvegetated landscapes have been computed by hand [144]!

Path Segmentation Analyses

One of the most active areas of research within movement ecology [56] is the development of methods to infer the behavioral state of individuals from relocation data. Some of these methods seek to segment movement paths into different behavioral phases (also known as canonical activity modes [69]), such as distinguishing between active and resting phases [15] or between foraging and traveling phases [55]. Segmentation methods may be based on threshold concepts [81, 162] or clustering methods [177]; or they may be based on geometric or periodic properties of the trajectory, as in *recursion* [11] and *wavelet* [191] analyses, respectively (Table 2.1).

One set of methods—*change point analyses* (Table 2.1)—are designed to detect changes in the movement behavior of individuals, and then relate these to environmental covariates [67] as possible causes for the behavioral shifts. These methods frequently use time-series analyses to identify notable shifts in the autocorrelations of the sequential values of primary or secondary metrics [79, 80]. Another set of methods—*state space modeling* approaches (Table 2.1)—are designed to identify a set of states (hopefully with a behavioral interpretation) underlying variations in movement behavior and, within the same analysis, determine the probabilities of switching among states. These methods attempt to assign "hidden behavioral states" to each location point, as well as a probability transition matrix that specifies the probability of an individual switching from one state to any other as the individual moves to the next location point. Essentially, the method produces a stochastic walk model, called a Hidden Markov Model (HMM; [132]). HMM movement trajectory models are complicated generalizations of random walks [123], where movement elements (step size and turning angle) depend on the current behavioral state, as does the probability of changing behavioral state when reaching the next location. To demonstrate the HMM method, we have analyzed the trajectory of a zebra using the `moveHMM` package [120] in the statistical analysis program R (version 3.4.3; [143]). The results obtained constitute the most probable decomposition of all of the 10,600 steps into a "two-state no-covariate model". The distributions of step lengths and turning angles associated with this model are depicted in Fig. 1.

Path or trajectory segmentation methods are one area of research common to both GIScience and movement ecology, with the GIS community supporting significant research on pattern-oriented, cross-scale, and cross-type segmentation methods [49, 5]. In a study designed to explore the role of uncertainty in trajectory and segmentation analyses, Laube et al. [99] fitted 10 cows with GPS collars taking sub-second fixes to investigate questions of scale, granularity, and uncertainty when working with GPS data to assess movement parameters. The results of this work should be of great interest to ecologists, who typically collect much coarser fix data and then either invoke a straight-line assumption about the nature of paths between any two consecutive points in their data or assume Gaussian diffusion, often relying on a Brownian Bridge method for constructing likely trajectories between such points [85].

Often limitations regarding the temporal resolution of movement data may require analysis at somewhat broader scales. Even at this higher level of abstraction, however, behavioral classification

may still be powerful. Indeed, Abrahms et al. [2] identified "movement syndromes" across 13 diverse taxa (marine and terrestrial) using five standard metrics (mean turning angle correlation, mean residence time, mean time-to-return, volume of intersection, and mean net squared displacement) and a principle components analysis. Although the trajectories studied varied in movement mode (e.g. flying, walking, swimming) and taxon, the analysis successfully differentiated among migratory, nomadic, central place foraging, and territorial behaviors from GPS data alone.

Alongside the development of analyses to derive behavioral states from GPS data, new tags and collars fitted with tri-axial accelerometers (and, often, additional sensors for light, barometric pressure, temperature, etc. [190]) increasingly allow for direct observation of the dynamic behavioral states of free-ranging animals [152, 184]. Using various machine learning algorithms, accelerometer data (in the form of three-dimensional movement generally at a 20-40Hz resolution) can be processed to classify basic behaviors (e.g. sitting, walking, diving, running, resting, foraging) across multiple taxa with high accuracy [127, 20, 60]. Although these algorithms require high resolution training data, often relying upon intensive observation of captive animals, this technology used in combination with GPS relocations can aid in the exploration of links among the biomechanical, behavioral, and ecological processes that influence whole-animal movement and contribute to a unified field of movement ecology [127].

Interactions

Although the majority of path trajectory analyses do not rely upon environmental covariates, often the results and interpretation of these metrics can be enhanced by assessing their environmental context. For example, taking account of the environmental context at a behavioral change-point can help researchers infer why an animal is changing behavior or what behaviors are being exhibited. Similarly, examining the environmental context alongside measures of first-passage time or residence time can be useful for understanding how animals relate to and behave in different environments. Inherently, the one-dimensional metrics we have highlighted here are applied only to individuals' trajectories. However, when aggregated across a group of animals, their results can be useful in distinguishing individual heterogeneity in a population or variation across species, just as done by Abrahms et al. [2] in their study of movement syndromes.

Emerging technologies, such as proximity collars, are advancing the study of conspecific interactions (and those among heterospecifics as well) along movement trajectories. The consideration of contacts among individuals moving across a given landscape can be vital for understanding the implications for resource use, competition, and disease transmission. Often interaction between two animals is assessed using point-based measures rather than integrating proximity across path segments, as in assessments of association coefficients or proximity analyses [111]. Recent advances in the GIS community, however, have led to improved methods for analyzing dynamic interactions (i.e. interactions that occur both in space and time using path-based metrics [110]). Often these interactions are translated into and analyzed as contact networks (an application of graph theory). However, since the majority of network analyses do not ask questions explicit to movement, we direct readers to alternative reviews of this growing area of research (e.g [40, 41, 136, 154]).

2.4 Space-Use Analyses

When scaling up from path-level to space-use analyses, movement ecologists employ a variety of metrics designed to evaluate how an individuals' movements, when viewed in the aggregate, partition the landscape in meaningful ways. Such two-dimensional constructions can explore how and when individuals use or share a given area or habitat in space or time with or without the consideration of the underlying environment. Below we explore these methods in two sections. First, we highlight methods based purely on movement metrics, irrespective of environmental context. These are generally used for characterizing the size and shape of animal home ranges. Second, we describe a suite of methods that combine movement locations with environmental covariates to make inference about habitat selection and the influence of landscape factors on space use.

Feature-independent analyses

Metrics analyzing the frequency of relocations across space regardless of environmental covariates broadly include the various methods for *home-range estimation*. These simple measures of animal space use (see Table 2.2) are applied widely, even with low-resolution data: though daily fix rates may prohibit fine-scale analyses such as behavioral state extraction, the aggregation of points at this resolution (over appropriate temporal spans) can easily inform the general size and shape of an animal's home range [194, 63, 62].

Several alternative methods for describing the home range of an animal exist, ranging in complexity from the construction of the *minimum convex polygon* containing the movement trajectory to a construction of a *utilization distribution* [180] that can be used to estimate the probability of finding an individual in selected areas inside the home range; see Fig. 2 for a comparison across three common methods for home-range construction. Most commonly, utilization distributions (UDs) are derived using kernel density estimators, now widely incorporated in many spatial analysis packages [194]. Subsequent development of other methods, based on Brownian movement models [85] and Local Convex Hull unions [70, 72, 112, 51], as well as autocorrelated kernel methods [64] have enabled more realistic or robust estimates of the utilization distribution. In order to delineate areas of most consistent use or offer conservative estimates of an animal's typical home range, researchers often include *isopleths* on maps of utilization distributions to identify the areas associated with a given percentage of relocations (e.g., 50%, 80%, or 95%). Utilization distributions can be calculated over any time interval of interest to delineate the space use of an animal over that time (e.g. a single month, a particular season, an entire year, etc.). By assessing the *volume of intersection* or overlap of successive short-term UDs for a particular individual, researchers can evaluate broad-scale site fidelity and ultimately the stability of an animal's home range ([63, 121, 35]; Table 2.2). Additionally, these same metrics can be used across individuals to estimate concurrent or shared space use, which can be important for understanding social structure, disease transmission, or competition for resources.

Within the utilization distribution, ecologists often define a "core area" of use. *Core area methods* refer to any one of a group of analyses that seek to identify the most intensely used areas from individuals' relocations histories. In their simplest form, these areas are defined as the smallest area incorporating some subjective percentage of relocations, generally 30-50%. Although widely

used, the selection of the 30% or 50% isopleth is ad-hoc. In an attempt to make this selection more rigorous, [181] propose researchers fit an exponential model to the rate at which home-range area increases for each percent increase in isopleth value; they define the core area as the point at which the slope of this exponential curve is 1. Other approaches involve integrating time-use patterns into the spatial analysis of movement data. In the simplest time-use metrics, researchers evaluate the *time to return* and the *return rate* (frequency of returns) to pre-defined areas in the home range, given some prescribed minimum time between "returns" [149, 179]. More elaborate methods incorporate time-use into the construction of the utilization distributions themselves [17]. The T-LoCoH method (implemented in R through the `tlocoh` package; [112]), for example, allows users to evaluate *revisitation* (a measure of separate visits) and average *duration of visits* (Table 2.1) to all local hulls within an animal's home range. These analyses can help elucidate spatial patterns in time strategies: teasing out not only what habitats animals are using, but also separating those they used in repeated short visits from those used for infrequent but extended visits.

In the GIS community, the competition in and for space and time that ecologists study as habitat selection or home range analysis, has often been considered as an extension of classic time geography [47, 108]. Various methods for illuminating space-time prisms, which map the potential movements of an object in both geographic space and time given information about its movement capabilities (e.g. travel velocity), can account for the time and sequentiality of measurements along movement paths. Extensions of these space-time prisms has resulted in methods for constructing 3-dimensional elements used to estimate the probability that an object was located at some location at some particular time. This approach offers a sophisticated technique for understanding the movements and activities (and potentially interactions) of animals at fine temporal and spatial scales [54].

All simple home-range estimators that ignore the temporal autocorrelation inherent in movement trajectories may be applied either to a single animal's trajectory or to a combined dataset across multiple individuals. Estimation methods that use the temporal nature of movement trajectories (e.g., autocorrelated kernel density methods, Brownian bridges, T-LoCoH), however, must be applied first to individual trajectories independently and subsequently combined if population space use is of interest.

Feature-dependent analyses

Methods used to construct *resource selection functions* (RSFs; [22]) are arguably the most utilized among spatially-explicit methods that incorporate environmental covariates (see Table 2.2). RSFs are typically employed to infer the probability of use of any given resource unit within the range of an individual or population, and thereby, represents the primary procedure for evaluating the selection of resources by both individuals and populations [22, 116]. Within the genre of habitat selection analysis, *step selection functions* (SSFs) function in a similar manner to RSFs, but are constructed at a much finer scale. These models compare habitat attributes at points along a given trajectory and estimate resource selection by comparing the environmental structure of the next point along the trajectory to other possible points available to the animal (taking into account step length and turning angle distributional structure). Thus, in short, SSFs offer a finer-scale

approximation of habitat selection along movement paths rather than the aggregate assessment yielded by a traditional RSF ([164]; see Fig. 3); however, we note that SSFs are sensitive to the frequency at which data are collected [68]. In fact, consideration of behavioral state, data collection, and fix interval (i.e., sampling frequency) is crucial to accurate representation of both habitat selection and connectivity [3, 2]. For example, when considering behavioral state in the evaluation of resource selection by African wild dogs, Abrahms et al. [3] demonstrated that the response of wild dogs to roads varied significantly depending on both the behavioral and landscape context in which roads were encountered.

Beyond estimating the probability of use of any given resource in space, ecologists and conservation biologists often want to evaluate the *connectivity* of a landscape for movement, both within and between populations. Metrics for assessing landscape connectivity are expansive, but the most common approaches involve various landscape pattern indices which serve to evaluate structural connectivity, a characteristic inherent to the landscape (see [165, 27, 58]). Functional connectivity can be calculated directly using movement trajectories [1, 3] or estimated indirectly using capture-recapture data [146]. For example, *least-cost modeling*, a popular analytical approach familiar to movement ecology and GIS alike, generates simulated paths based on estimates of the efficiency with which an individual could move between two points. Efficiency can be a function of distance, time, or any other weighted resistance layer. Traditionally, maps of *landscape resistance* have been generated from a mix of expert opinion, previous studies, species presence locations, habitat suitability indices (often also derived by expert opinion), and radio-telemetry points [147]. More recently, these maps have been generated using circuit theory [119] or by using the inverse of selection functions, thereby integrating actual movement paths into the assessment of landscape permeability [34, 198].

Often in the study of movement, dynamics within a population of animals, rather than those of a single individual, are of primary interest. As such, although both landscape connectivity and habitat selection analyses can be run on single trajectories, it is most common to run these analyses on groups of individuals to infer population-wide behaviors. Of course, without comprehensive tracking of all individuals in a population, general conclusions can be difficult to draw or, when formed from empirical observation on a subset of the population, biased due to individual and environmental heterogeneity (especially with small sample sizes). However, as GPS technology has become more cost-effective and widely available, researchers with appropriate sampling schemes and investigating data from multiple individuals within a population can begin to draw conclusions about general space use and effectiveness of management strategies for a population or species.

2.5 Bridging Perspectives

In Ecology at Large

As a sub-discipline within ecology, movement ecology often has a somewhat narrow focus, considering foundational questions such as when, where, how, and why animals move [126]. Indeed, despite its interdisciplinary origins, movement ecology tools are often used for 'basic' science (i.e., addressing research questions without specific applications beyond the creation of new knowledge about a system) in contrast to GIScience's often more applied focus. But the methods of movement

ecology draw on several disciplines, including physics, biomechanics, behavioral ecology, landscape ecology, and GIScience. Moreover, at its core, movement ecology is a means of cutting across scales, linking the mechanical and physiological basis of behavior to continental-level patterns in animal distributions. That cross-scale nature allows movement ecology to be adaptable and flexible for solving real-world problems in human-dominated landscapes.

In conservation biology, movement tools have clear and well-tested applications for both policy making and wildlife management. In particular, movement ecology provides an invaluable framework for understanding, measuring, and predicting human-wildlife conflict. For instance, Mountrakis & Gunson [125] used kernel density estimation to evaluate spatiotemporal hotspots where the risk of moose-vehicle collisions may be high. Further, in a study investigating the space-use behavior of leopards in human-dominated landscapes, Odden et al. [129] found that home-range size was markedly smaller and movement patterns (as defined by *step-length* distributions) more nocturnal for leopards ranging closer to human settlements, results that reflect a behavioral shift that may reduce conflict. Movement tools can also be used to plan and optimize mitigation efforts, like highway overpasses and conservation corridors, and provide a means to evaluate the success of management decisions. Indeed, policy for dealing with conflict can be expensive and retaliatory [118], resulting in the death of endangered animals in an often misguided attempt to prevent future conflict. In the case of leopards in India, for example, the common management practice of haphazard capture and relocation of problem animals has been shown to be counterproductive; although translocations may provide temporary local relief, they were found to increase the subsequent overall level of conflict [9, 129].

Movement research also has tremendous potential for addressing complex challenges where movement is only an implicit part of the problem. In recent years, movement data has become an increasingly valuable asset in disease ecology, with the vast majority of emerging human health threats connected in some way to the human-wildlife-livestock interface [89]. Movement already plays a key role in disease ecology, with many researchers interested in answering clear-cut questions like whether host movement behavior changes their risk of disease, or whether infection alters host movements. Movement tools are particularly useful for illuminating aspects of individual heterogeneity that may directly influence exposure and transmission processes; effective incorporation of such knowledge into existing (or adapted) epidemiological models may result in a framework that offers more accurate predictions of spatiotemporal disease dynamics [52]. In an example of this, research into the spatial organization of badgers (*Meles meles*) has demonstrated that culling, a widespread government control method for tuberculosis, can have an adverse effect—and actually increases contact between badgers and cattle [192]. In the future, more real-time applications may become increasingly prevalent not only in forecasting but also in surveillance, for example, in efforts to prevent spillover of bat-borne viruses like Ebola and Nipah.

Further, although our focus here has been on analyses for GPS relocation data, in most cases the metrics and methods presented may be used to assess other kinds of geospatial data. In fact, many of the tools explored here have applications outside movement ecology and beyond the conservation and disease ecology considered here. These tools have considerable potential for facilitating cross-disciplinary research. For example, cluster analyses used in movement ecology to identify, *inter alia*, kill sites and foraging patches [163, 149, 185] were originally developed by researchers to identify

disease hotspots from disease-incidence records [95]. In the same vein, resistance mapping and network analyses have clear implications for assessing transportation and traffic flow.

Outside Ecology

Many of the questions and methods used in movement ecology are not unique to animal behavior. As the digital traces on human lives have multiplied (e.g., via mobile phones, geo-tagged social media), the field of human mobility analysis (HMA) has become an increasingly important part of sociology and human geography [33]. Movement ecology may be able to learn from the experience of GIS and HMA communities, as the streams of passive data available from mobile phone records and social media have already eclipsed those available to ecologists by several orders of magnitude. Models and techniques used in HMA and movement ecology often ask similar questions (e.g. can we infer activity or behavior from movement patterns?) and are motivated by a shared foundation in physics and mathematics (e.g. diffusion models and stochastic processes; [77]).

Although the two fields often approach these questions at different scales, with different applications and impact, and using different nomenclature, movement ecologists can learn as much from this realm as geographers may take from movement ecology, especially as the resolution of available animal movement data increases to match that of HMA. In the future, both of these fields will face challenges to develop new methods and metrics to handle the proliferation of "big data" as movement tracking becomes lighter, easier, and cheaper to implement, and involuntary data collection becomes more ubiquitous for human mobility [94]. Further, the historical frameworks in transportation research for active data collection, using surveys and GPS loggers, can offer powerful means for validating new models and methods that would be unavailable in wildlife research [32].

It is worth noting in this context that quantitative models and approaches can only go so far, and behavior—human or animal—has limited predictability [159, 158]. Qualitative data and systems to collect and analyze them—a realm that has been advanced by human geographers and political ecologists who seek to document and understand the spatial nature of institutions and policy—can help to fill in some of the gaps and bring greater understanding to the motivations and patterns behind movement and human behavior more generally. In this vein, the application of qualitative data is yet another area where movement ecology can benefit from an integration with GIS. As there are no landscapes that remain untouched by humans, qualitative data and perspectives should be considered crucial not only to human research but also to the understanding of ecological systems. Research at the interface of ecology and human geography has the potential to enhance our understanding of both the social and ecological impacts of global change (e.g. [82]).

The shared questions and challenges facing GIS and movement ecology may help facilitate fruitful collaboration in the future, especially if undertaken with a shared commitment to open science and its infrastructure, open data, and the development of open source tools on both sides. Though proprietary software, such as ESRI ArcGIS, is regularly used by ecologists, the community is moving toward open source solutions. Many of these tools are developed and maintained by the GIS community's own open geography advocates and organizations (OsGeo); open source GIS software packages like GRASS and QGIS and spatial libraries in R and Python are becoming more developed and widely used. However, open data sharing is often a bottleneck in both fields. Political,

legal, and privacy issues with sharing data, especially when human subjects are involved, generally limits open data availability [46, 161]. However even in movement ecology, data archival or sharing has been slow to take hold, even with the existence of community-specific infrastructures, such as Movebank, developed for the purpose [189]. Continued investment on both sides of GIScience and movement ecology can help guide wider dissemination of these tools and the successful integration of the two fields.

2.6 Discussion

Today, movement data are collected at increasingly high resolutions of time and space. This explosion of data demands new methods and techniques to analyze them efficiently [109]. Likewise, improvements in technology for tracking animal movements has increased demand for toolkits able to extract the behavioral and ecological factors behind animal movement and space use. Here we have outlined a selection of methods for exploring movement data of free-ranging animals that can answer animal behavior questions across scales, particularly as they may relate to conservation and wildlife disease issues.

As has been noted, GIS is fundamentally based on the study of geographic information in the context of processes that enhance spatial knowledge and support decision making, often on a global scale [196]. It thus follows that GIS and movement ecology overlap where environmental and landscape factors are considered in the context of space use by individuals and populations. Although we have limited our review to applications of single population or community analyses, studies of whole species distributions or long term range shifts [57, 8] are representative of active areas of research in ecology. These distributions are rarely linked to movement ecology even though they naturally emerge from animals' individual movement decisions [91]. No matter how climate suitability shifts over time, the ability of species to track changing climates ultimately depends on their dispersal ability—but in global change biology, this is most commonly reduced to a single maximum upper rate [170]. Movement ecology is on track to play an increasingly important role, not just in refining those predictions, but also in tracking species' actual responses in real time.

In short, many of the questions addressed in movement ecology overlap with those being asked throughout the broader GIS community: questions relating to geospatial data analyses that address the behavior of individuals, the demography of populations, and the structure of landscapes in the face of global change. Given this overlap, we are confident this review will help stimulate further transdisciplinary and interdisciplinary research among ecologists and geographers.

2.7 Tables

Table 2.1: Path Metrics & Ensuing Methods

Metrics	**Description**	**Suggested References**
Step size (length)	The displacement between two consecutive coordinate fixes	[30, 172]
Heading (or absolute angle)	The direction of heading relative to some standard (e.g., initial direction, compass North)	[30, 172]
Turning angle	The change in heading from one step to the next	[30, 172]
Displacement	The straight-line distance from the beginning to the end point of a path	[30, 172]
Net squared displacement (NSD)	The square of the straight-line distance between the start of the trajectory and the current location	[30, 172]
Persistence velocity	The speed of movement in the direction of heading	[79]
First passage time	The time taken to exit a circle of prescribed radius r from a relocation point at the center of this circle	[59, 117]
Straightness index	The ratio of $\sqrt{\text{NSD}}$ to the path length (sum of the step sizes) of the trajectory segment of interest	[16]
Tortuosity	The level of convolution in a movement path relative to a straight line	[16]
Residence time	The amount of time spent within a selected area	[12]
Return time (inter-visit gap)	The amount of time it takes an individual to return to a particular area after its last departure	[112]
Revisitation (or return) rate	The rate at which an individual returns to a particular area, where distinct visits are based on a minimum return time t_r	[112, 179]
Mean duration	The average amount of time spent per visit over a number of visits to a selected area	[112]
Time to return	The duration of time between consecutive visits to a selected area	[11]
Overall dynamic body acceleration (ODBA)	The sum of the absolute values of three orthogonal locally time-averaged accelerations	[75, 142]
Behavioral state	Association of one of several discrete modes of behavior with each point on the trajectory	[69]
Methods (in the context of movement ecology)		
Cluster analyses	Methods for grouping trajectory points (or segments) that represent the same behavioral state (or syndrome)	[177] (or [2])
Change-point analyses	Methods for detecting points on a trajectory where switches in behavioral states occur	[79]
State-space analyses (hidden Markov models)	Methods for detecting underlying behavioral states and estimating state transition probabilities	[132]
Accelerometry visualization	Using tri-axial accelerometer data (e.g., OBDA) to evaluate behavioral states	[152]
Wavelet analysis	Method for detecting periodically varying movement and behavior patterns across all temporal scales	[140]
Recursion analyses	Methods for detecting movement trajectory recursions (returns to prior locations)	[18]

Table 2.2: Space-Use Metrics & Methods (in the context of movement ecology)

Featureless Landscapes	**Description**	**Suggested References**
Home range estimation	The estimation of habitually-used areas with function-dependent boundaries (e.g. summer range, defended territory, core territory). Most commonly accomplished using densities of use calculated from estimates of the animals' locations across a landscape	[141, 62]
Utilization distribution	Relative frequency distributions of an animal's location over space for a specified period of time	[194]
Home range fidelity	Measures of home-range overlap among individuals (e.g., volumes of intersection) and home-range stability over time	[63, 121]
Core area methods	Analyses for identifying areas of most consistent use/selection from individuals' relocation histories	[181]
Conspecific proximity methods	Methods for estimating and characterizing the interactions among and impact of conspecifics on movement trajectories	[45]
Featured Landscapes		
Resource selection functions (RSFs)	Statistical models producing values proportional to the probability of use of a resource unit. RSFs are often constructed using a logistic regression framework comparing points used by an animal to those "available" to it within its home range	[116, 22]
Step selection functions (SSF)	A model of resource selection that includes movement behavior to constrain selection and availability. In an SSF, each step at time t is paired with one or more random steps with the same starting point drawn at random from a distribution of step lengths and turning angles.	[164]
Landscape resistance	Measure of the relative difficulty (e.g., energy used per unit distance moved) for individuals to move as a function of topography and environmental features	[197]
Least cost methods	Analyses for finding the least difficult (least energy expended) path between two points. May be extended to avoid risks of encountering competitors, predators, etc.	[183, 4]
Circuit theory	An application of electrical circuit theory to model landscape connectivity and resistance through graph and random walk theories	[119]

2.8 Figures

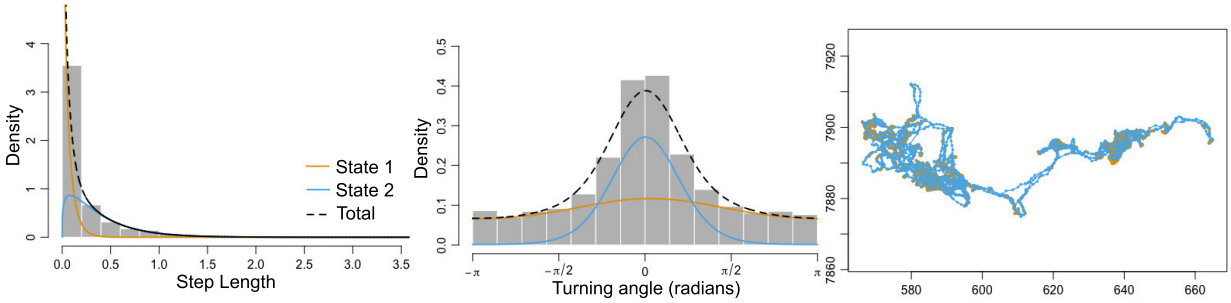

Figure 2.1: **Results of a "2-state, no-covariate" behavioral model of zebra "AG256"** using the `moveHMM` package in R (see supplementary files for data and code). This analysis assumed 2 distinct behavioral states and included only an intercept term, no environmental or other physiological covariates were included. Panels (a) & (b) show the empirical distributions of step lengths and turning angles respectively, using yellow and blue lines to depict the estimated distributions in each behavioral state. Panel (c) displays the particular trajectory used to produce distributions (a) and (b), with each color-coded with respect to their predicted behavioral state: yellow for state 1 and blue for state 2. Data exploration and biological knowledge of the observed individual is necessary to determine whether a model with more than two states clarifies or muddies interpretation of what each state is likely to represent. In our example, it seems probable, given the relatively uniform distribution of turning angles and the high density of short steps, that State 1 represents bouts of foraging while State 2 represents more directed movement behavior (e.g., travel; notice the apparently unbiased distribution of turning angles and larger step sizes).

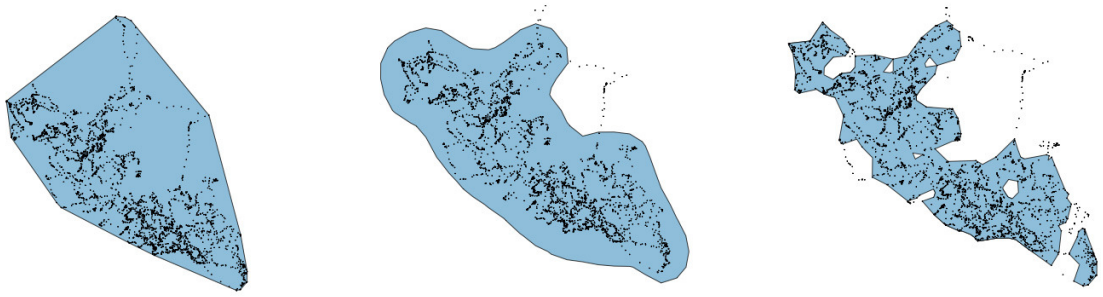

Figure 2.2: **Comparative home range estimates for zebra "AG256"** (using only the data that pertains to the western part of its total range—cf. Panel (c) in Fig. 1) across 3 static (i.e., time-integrated) techniques. The simplest technique, a minimum convex polygon (MCP), displayed in Panel (a), defines the extent of a home range as the smallest convex polygon fitting a given percentage of points. Though still used widely, MCPs are criticized as poor estimators of an animal's true home range because they often contain large areas unused, and potentially unavailable, to the observed individual, as evident in the upper-center of our trajectory. Panel (b) displays a common alternative: the 95% kernel utilization distribution. This method was developed to more rigorously quantify an animals actual space use and ultimately defines an animal's home range as a bivariate probability density function, calculating the probability of relocating an animal in any given location [194]. Panel (c) offers a non-parametric approach, calculating the home range of the zebra using a-LoCoH, the adaptive local convex hull method developed by Getz et al. [72] that constructs kernels at each relocation using all points within a total distance a such that the distances of all neighboring points to the reference point sum to a value less than or equal to a. In our example, we used $a = 75000$ m, which provided a contiguous range that trades-off fewer false positives at the expense of more false negatives than the other two methods. There is much debate and continued development in the area of home-range estimation and researchers must be conscious of the differences across metrics, because results often vary widely and may offer different biological interpretations (e.g., defining the extent of the habitat available to the animal for selection versus the area traversed in daily activity [62]). For more detail on the construction of these three home range measures, see supplementary information.

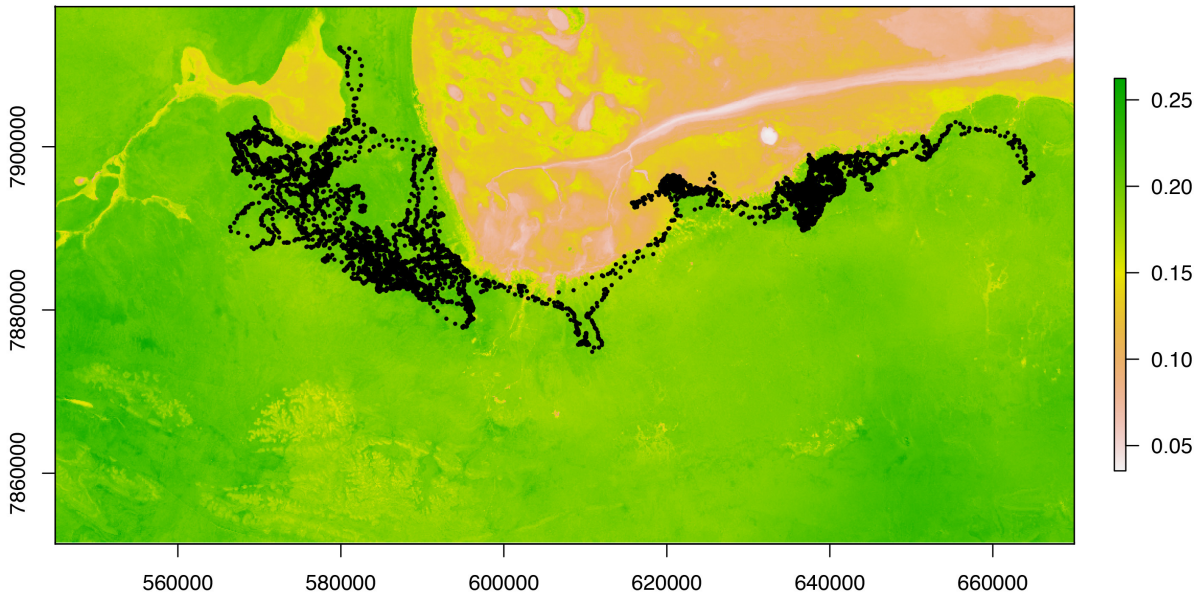

Figure 2.3: **Predicted habitat selection using a step-selection function for zebra "AG256".** Fundamentally, selection functions calculate the selection ratio of any given resource unit by comparing characteristics of "used" units to those "available" to the animal, typically using a logistic regression framework. Step-selection functions differ from traditional RSFs by defining what is "available" according to randomly drawn steps from each point rather than a simple random sample of the home range as a whole. Here we display AG256's predicted selection ratio for a portion of Etosha National Park according to 4 environmental layers: distance to primary roads, distance to functional water sources, mean greenness, and mean wetness. On top of the predicted selection layer, the original trajectory is plotted in black. Note that only the western part of the trajectory, which occurs during the wet season [199], is used to construct the home ranges depicted in Fig. 2.2). For a complete discussion of the regression and details regarding the selection of available steps and the environmental layers used, please see supplementary information.

2.9 Supplementary Materials

Details regarding empirical trajectory used

All example analyses were run on a single trajectory from zebra AG256, a free-ranging female zebra collared in Etosha National Park, Namibia. Data were collected from AG256 from October 2009 through August 2010 in an intentionally irregular manner (two fixes separated by one minute, then a third 19 minutes after that). Before analysis, this trajectory was regularized using the `adehabitatLT` package such that only the first and third fix of each set remained, thereby resulting in relocations every 20 minutes. Additionally the trajectory was cut to include only the 10800 points from February through June 2010 to limit the dataset size for rapid analysis and because this time period corresponds with the wet season in Namibia. For the purpose of the home range analyses, this trajectory was further trimmed to only the 4247 points from February 15, 2010 - April 15, 2010 while AG256 remained in the western part of her range.

Details on example analyses

A link will be provided to all data and analysis code according to our Data Availability statement upon acceptance after anonymous review.

Home Range Analyses

Minimum Convex Polygon

The 100% minimum convex polygon was calculated using the *mcp* function within the `adehabitatHR` package in R.

Kernel Utilization Distribution

The 95% kernel utilization distribution was calculated using the *kernelUD* and *getverticeshr* functions within the `adehabitatHR` package in R. The *kernelUD* function was implemented using the default bivariate normal kernel and default smoothing parameter calculation. Please see the adehabitatHR manual for more information regarding this functions implementation. 'getverticeshr' was then used to extract the 95th percentile contour for plotting.

Local Convex Hull

The 95% local convex hull union was constructed using the `tlocoh` package in R with parameters $a = 75000$ and s=0. The a-LoCoH method creates convex hull sets from the maximum number of nearest neighbor points such that the sum of their distances from the point of interest is less than or equal to a. To select the appropriate a value, we examined the resulting hullsets and investigated plots of a vs. isopleth area and a vs. isopleth edge-area ratio for a values from 30,000 to 80,000 at intervals of 5,000. For more information about the appropriate selection of LoCoH parameter values, please see [72, 112, 51].

Behavioral State Analysis

After projecting the zebra trajectory (WGS84 UTM Zone 33S), the step lengths were transformed from meters to kilometers. A two-state model with no additional environmental covariates (a "two-state, no-covariate" model) was fit to the data. The initial values for the Gamma (step length) and von Mises (turning angle) distributions are in Table 2.3 whereas the final estimates are displayed in Table 2.4.

Table 2.3: Initial parameter values for the Hidden Markov Model

Step Lengths (Gamma)			**Turning Angles (vonMises)**	
mu	sigma	zero-mass	mean	concentration
0.1	0.1	1	π	1
1	1	0.05	0	1

Table 2.4: Parameter estimates for the Hidden Markov Model

Step Lengths (Gamma)			**Turning Angles (von Mises)**	
mu	sigma	zero-mass	mean	concentration
0.049	0.062	0	0.096	0.286
0.381	0.338	0	0.010	2.728

Step Selection Analysis

Selection of available points:

Step length and turning angles were calculated for each step in the empirical trajectory of AG256 using the `adehabitatLT` package. To inform the regression analysis, five 'available' points were sampled for each 'used' point. Sampling was achieved by randomly selecting paired sets of step lengths and turning angles observed in the empirical trajectory. By maintaining the step lengths and turning angles in pairs, we can maintain the behavioral mode underlying each step.

Environmental layers:

- **Landsat 4-5 TM - Greenness** Calculated based on the tasseled-cap transformation equation presented by Crist & Cicone [39], which utilizes 6 of the 7 bands in a regression framework to calculate several measures, including Greenness, Wetness, and Brightness. Resolution: 30 meter.

- **Landsat 4-5 TM - Normalized Difference Vegetation Index (NDVI)** Resolution: 30 meter
- **distance to functional water**
- **distance to primary roads**

Regression:

Available and used points were given a binary variable for identification (1 for used, 0 for available) and combined into a single dataset. Values of each of the 4 environmental layers were extracted at each point using the extract function in the `raster` package. The resulting dataframe was passed to the *glm* function in package `lme4` and a binomial logistic regression with a logit link was run:

$$Used \sim \beta_0 + \beta_1 * distRD + \beta_2 * distH2O + \beta_3 * Greeness + \beta_4 * NDVI$$

The resulting model fit was fed into the *predict* function (in the package `raster`) and used to predict the selection ratio for the full extent of all 4 environmental layers. This predicted layer is what is displayed in Figure 3. Fitted coefficients of the model can be seen in Table 2.5.

Table 2.5: Fitted coefficients from example SSF

Coefficients:	**Estimate**	**Std. Error**	**z value**	**P value**
(Intercept)	-1.859e+00	5.558e-02	-33.447	<2e-16 ***
Dist_PrimaryRoads	5.863e-06	5.698e-06	1.029	0.30353
Dist_Water	-5.785e-06	2.195e-06	-2.636	0.00839 **
Mean_Greenness_2010	7.462e-03	1.328e-03	5.618	1.93e-08 ***
Mean_Wetness_2010	-6.962e-03	1.174e-03	-5.931	3.00e-09 ***

[1] Significance codes: 0 '***' 0.001 '**'

Table 2.6: A selection of current R packages for spatial data analysis

Desired Analysis/Function	**Selected Packages**
Importing, manipulating, projecting spatial vector data in R	`sp, sf, rgeos`
Importing, manipulating, projecting raster data in R	`raster, velox`
Plotting spatial data in R	`ggplot2, mapview`
Behavioral state analysis in R	`moveHMM, bcpa`
Manipulating movement data in R	`move, adehabitatLT, BBMM, ctmm`
Home range estimation in R	`adehabitatHR, tlocoh, move, BBMM, ctmm`
Habitat selection in R	`lme4, adehabitatHR`
Connectivity in R	`grainscape, gdistance`
Dynamic interaction analysis in R	`wildlifeDI`

Chapter 3

Mesoscale movement and recursion behaviors of Namibian black rhinos

Dana Paige Seidel Wayne L. Linklater Werner Kilian Pierre duPreez Wayne M. Getz

Originally formatted for submission to a Special Edition Issue *Movement Ecology* and reproduced here with the permission of Wayne L. Linklater, Werner Kilian, Pierre duPreez, and Wayne M. Getz.

3.1 Abstract

Background Understanding rhino movement behavior, especially their recursive movements, holds significant promise for enhancing rhino conservation efforts, and protecting their habitats and the biodiversity they support. Here we investigate the daily, biweekly, and seasonal recursion behavior of rhinos, to aid conservation applications and increase our foundational knowledge about these important ecosystem engineers.

Methods Using relocation data from 59 rhinos across northern Namibia and 8 years of sampling efforts, we investigated patterns in 24-hour displacement at dawn, dusk, midday, and midnight to examine movement behaviors at an intermediate scale and across daily behavioral modes of foraging and resting. To understand recursion patterns across animals' short and long-term ranges, we built T-LoCoH time use grids to estimate recursive movement by each individual. Comparing these grids to contemporaneous MODIS imagery, we investigated productivity's influence on short-term space use and recursion. Finally, we investigated patterns of recursion within a year's home range, measuring the time to return to the most intensively used patches.

Results 24-hour displacements at dawn were frequently smaller than 24-hour displacements at dusk or at midday and midnight resting periods. Recursion analyses demonstrated that short-term

recursion was most common in areas of median rather than maximum NDVI values. Investigated across a full year, recursion analysis showed rhinos most frequently returned to areas within 8-21 days, though visits were also seen separated by months likely suggesting seasonality in range use.

Conclusions Our results indicate that rhinos may frequently stay within the same area of their home ranges for days at a time, and possibly return to the same general area days in a row especially during morning foraging bouts. Recursion across larger time scales is also evident, and likely a contributing mechanism for maintaining open landscapes and browsing lawns of the savanna.

3.2 Background

Movement ecology holds considerable promise for understanding rhino ecology and their conservation. However, an ISI Web of Science keyword search using “movement ecology” and “rhinoceros" yields no published studies. Make the same search for elephant or whales and many published studies appear. It is interesting to contemplate why rhino are so much less studied in this regard. Foremost among the reasons is probably that elephant and whales range over great distances and migrate, thus making movement a more obvious feature of their ecology and germane to their conservation and management. Rhinos, however, are attached to comparatively small home ranges with intensively used core areas [78]. Movement ecology studies of other large herbivores that are similarly sedentary, such as giraffe and hippopotamus, are also scant. Fitting GPS collars to rhino has also proved more difficult [84] and controversial [6, 167] than many other species, including elephants. Rhinos do not have slender necks to hold a collar between their heads and shoulders; and they treat their collars roughly, breaking them on the vegetation and rocks on which they push and rub, or reducing satellite antennae functionality through a coating of mud when wallowing. Until recently, rhino movement studies were limited to short-range horn-implant transmitters [153, 107] that yielded comparatively small amounts of discontinuous movement data. These studies, however, provided movement data at both the micro (step-by-step foraging) and macro (seasonal ranging) scales, but not at the meso (daily or weekly) scale.

The study of movement is central to addressing the challenges of rhino species conservation because recovery now depends on growing and managing meta-populations in, largely fenced, wildlife reserves that are networked by rhino translocations for reintroduction and restocking. For example, simulating source-sink dynamics in the larger reserves has met with some, but mixed, success for rhino [71]. Evaluating its usefulness and limitations depends on our understanding of rhino movement, particularly dispersal [106]. Where an entire population is a donor for the meta-population, rapid compensatory reproduction depends also on dispersal and range recolonization [106]. Moreover, mitigating the significant environmental and social risks inherent in rhinos’ release into unfamiliar habitat and populations [107] depends also on anticipating the movement behavior of released individuals. Concern exists that competition with elephant [156] and calf depredation by large predators, such as spotted hyena and lion [137] might slow species recovery. Rhinos’ movements in relation to competitors and predators could be revealing and may address such concerns. Studies of home range have been crude and analyses are still plagued by facile comparisons [105, 138] that would be greatly improved by meso-scale movement analyses. Lastly, and perhaps most

importantly, rhino habitat is increasingly shared with people and their infrastructure. They may be in rhinos' habitat to view or hunt them or other wildlife, or they may be poachers. Rhino poaching continues to be the largest cause of population decline and places the greatest limits on rhino species recovery [61]. Movement of individual rhinos in response to encounters with humans, whether they be tourists or hunters, sanctioned or illegal, promises to facilitate co-existence and persistence in rhino habitats that are increasingly anthropogenic.

Movement has been particularly central to studies of rhino food and habitat choice, and the configuration of home ranges and territories. At the micro scale, feeding tracks have been the mainstay of monitoring and research for several decades, most often to understand food preferences [148, 130, 103]. More than other large mammals, rhinos' micro-scale movements have been studied because of the ease with which individuals could be identified and tracked over sandy or muddy substrates that constitute the landscape of many rhino populations [88, 100]. At the macro-scale, the description of home ranges or territories, especially using horn-implant transmitters, has also been common and applied to understand habitat requirements [76, 83, 187, 138]. Nonetheless, missing from the literature on rhino is an understanding of movement at the meso-scale and thereby constricting our ability to answer the questions: How do micro-movements translate into home ranges and spatial-use patterns? Are rhino spatial and temporal movements cyclic? Can we use rhino movement to understand ecological processes other than foraging? Research on black rhino is yet to take best advantage of the tools and ideas of the (relatively) young sub-discipline of movement ecology.

Despite the need and opportunity, the application of concepts and tools from animal movement research to understanding rhino ecology and conservation has not advanced appreciably since the literature was last reviewed over 15 years ago [104]. Our understanding of the fundamental ecology of rhino movement is still rudimentary in that it relies largely on anecdotal observations at the micro- and macro-scales, rather than extensive sets of movement data. For example, it is routinely assumed that rhinos' movements are driven by resource heterogeneity and optimal foraging of resource patches. We might expect, therefore, meso-scale movements to be bimodal, whereby short distance movements within patches are punctuated by fewer longer-distance movements between patches, especially in more arid environments. It is also assumed that daily drinking at a few sources of standing water, mostly soon after dusk or before dawn [148], causes rhino movements to be circuitous around waterholes. It is also known that rhino are crepuscular and thus assumed that the movement cycle is during active, mostly feeding periods around dawn and dusk. What is not known is whether daytime or nighttime feeding cycles generate more displacement and to what degree resting sites, such as waterholes, create centrality in meso-movement patterns.

Furthermore, rhinoceros, like other mega-herbivores, are considered to be ecological engineers [131] based on their potential to impose spatial and temporal heterogeneity on landscape vegetation structure and regulate other causes of disturbance, such as fire. For example, evidence suggests that white rhino grazing imposes vegetation heterogeneity on the landscape by creating grazing lawns. Those lawns appear to facilitate feeding by other smaller-bodied grazers and regulate fire extent and intensity [182]. A similar effect has been suggested for large browsers [115, 65, 42], such as black rhinoceros. Hedging of its favoured browse may make trees and shrubs more productive and prevent their growth into inaccessible height classes and vegetation succession towards a canopy.

Thus, rhino movements should betray recursive movements, returning individuals repetitively to the same feeding areas with elevated productivity and biodiversity. Recursion may be critical to understanding rhino impact on habitat structure and ecosystem function, however, to our knowledge, this has not yet been rigorously studied using GPS relocation data from continuously monitored individuals.

In this manuscript, using a unique relocation dataset for 59 black rhinos (*Diceros bicornis*) ranging across national parks and community conservation parcels in northern Namibia, we seek to answer some of these questions, evaluate long-held assumptions, and build an empirical understanding of rhino recursion across scales. To begin, we explore 24-hr displacement cycles at times of day associated with foraging and resting to understand daily movement behaviors and inspect tracks for evidence of circuitous movement. Secondly, we identify areas across rhinos' ranges with high recursion or long-duration visits and explore how spatial-distribution of resources (i.e. functional water and productivity) may influence rhino movements and subsequent home range development. By exploring meso-scale movement in rhinos, our goal is contribute new foundational knowledge of rhino ecology and to identify useful next questions for future research of this important and threatened species and the biodiversity they both represent and support.

3.3 Methods

Telemetry data and study area

The rhinos in this study had ranges in northern Namibia, in the unfenced Kunene Region to the west, in Etosha National Park to the east and in Waterberg National Park to the southeast. The ranges occur in several distinct ecoregions and across a marked precipitation gradient with the western coast being significantly dryer than the eastern region (Fig 3.1; [48]). GPS locations were acquired from multiple studies across two sampling periods and multiple rhino clusters. All rhinos were fitted with IR-SAT Iridium satellite foot bracelets with GPS and UHF (AWT Wildlife Tracking, Pretoria, South Africa). Rhino immobilization was done from a helicopter by veterinarians from the Ministry of Environment and Tourism, Namibia. The capture, collaring and transportation (when necessary), of rhinos was done following Standard Operating Procedures in compliance with the best veterinary practices.

Our dataset includes relocations from 59 individual rhinos: 41 individuals were sampled between October 2011 and January 2014 and an additional 18 individuals were sampled between July 2017 and November 2018 (Fig. 3.2). Four rhinos ranged within Waterberg National Park, all of which were sampled in 2013. Sixteen individuals ranged freely to the west and south of Etosha National Park boundaries in community-based conservation lands. Finally, relocation data from across the full expanse of Etosha National Park was collected from 39 individuals. Thirty-eight of the rhinos were female, with 15 of those identified as pregnant or accompanied by a calf at capture. 20 rhinos were male and the sex of one individual was not recorded.

As is common among rhino telemetry studies, fix rates across all individuals were irregular ranging from roughly 1 fix per hour for some individuals to less than 3 fixes per day for other

individuals. All trajectories had some degree of fix lag, missed fixes, or inconsistent fix rates whereby regularization would result in observation loss and interpolation methods would likely have biased movement analyses. Therefore, analyses were chosen and results interpreted with data irregularity in mind. Coordinates for 63 known waterholes across Etosha National Park were used in analyses to evaluate hypothesized recursion behaviors. All data manipulation and analyses were done in program `R` (v. 3.5.1) [143].

24-hour displacement cycles

Rhinos are known to be crepuscular creatures, with their most active feeding periods around dawn and dusk and their longest period of rest during the heat of midday. To investigate whether daytime or nighttime feeding cycles generate more displacement and to what degree resting sites or resources, such as waterholes, create centrality in meso-movement patterns, we began by standardizing individuals' daily fixes to roughly 6 hour intervals represented by a fix at "dawn" (07:00 ±2:30), "midday" (13:00 ±2:30), "dusk" (23:00 ±2:30), and "midnight" (23:00 ±2:30). Because of the considerable variation among collar fix rates, we liberally interpreted a fix as within 2.5 hours of each nominal time of interest. If there were multiple fixes within the interval, we selected the one closest to the hour of interest. For example, a rhino with a fix at 5:45 am and no other before 9:30 am would have this fix recorded as a "dawn" fix for that day. Using this standardized dataset, we then calculated the displacement between each ≈ 12 hour interval (e.g., dawn to dusk), and ≈ 24 hour interval (e.g., dawn to dawn).

For initial analyses, we selected 9 individuals with at least 30 days consistent fixes at likely foraging hours dawn and dusk. We then plotted the 24-hr displacement time series (calculated from dawn to dawn) for each individual and visually inspected for periodicity. Additionally, we built and visually inspected density plots for 24-hr displacement measurements as measured from dawn to dawn and dusk to dusk. We hypothesized that daily displacement by rhino individuals would demonstrate a bimodal frequency distribution indicating support for day-to-day movement patterns that include high rates of short-term residency interspersed with occasional long distance movements to new parts of the greater home range. To further investigate our hypothesis, we repeated our analyses using the complete data set: i.e., requiring no daily consistency and calculating distances for any complete pairs of points. With this data we additionally calculated displacement at an ≈ 6 hour interval (e.g, dawn to midday) to allow us to investigate resting cycle displacement for comparison. Since rhinos are known to visit waterholes daily to drink, mostly soon after dusk or before dawn [148], we hypothesized that dusk and dawn displacement would be more conservative than resting period displacement. In other words, we expected that daily recursion to waterholes, tied to hydration demands, would result in a high frequency of smaller displacement measures. To further evaluate our hypotheses regarding waterhole use, we calculated the frequency of points from each time of day within a 500m radius of known waterholes in Etosha National Park. A two-sample Kolmogorov–Smirnov test was used to test for differences across empirical 24-hr displacement distributions. Daily displacement patterns were additionally investigated across wet (November - March) and dry (April - October) seasons and between the sexes. Seasons were determined using rainfall data sampled from 7 sites within Etosha National Park in 1981-2013.

Biweekly recursion analysis

For optimal foragers, patch visitation and revisitation on spatially heterogeneous landscapes is thought to be driven, in part, by the productivity cycle. Feeding in a patch leads to local resource depletion, potential individual satiation, and optimal patch-leaving decisions [31, 160]; after the animal leaves a patch, environmental resources replenish incentivizing revisitation [178]. It's this visitation cycle, when done by rhinos or other megaherbivores, that is thought to be a mechanism for browsing lawn maintenance and prevention of canopy growth. To estimate how landscape structure and productivity may influence rhino movement and short-term patch recursion, we downloaded 16-day, 250 m^2 resolution, composite images from MODIS satellites using NASA's earthdata search for all 16-day intervals in 2011-2018 and extracted the NDVI product layer. The Normalized Difference Vegetation Index (NDVI), is a commonly-used, remotely-sensed measurement of productivity and an index of canopy cover. Previous studies have shown a linear relationship between NDVI and percentage vegetation cover, with increased correlation to canopy structure (i.e green biomass, green leaf area index) in areas of sparse canopy [66, 166].

To estimate patch recursion, we divided individuals' trajectories into 16 day intervals aligned with MODIS satellite collection periods in each year of sampling. Using the `tlocoh` and `tlocoh.dev` packages [113, 114], we built time use grids for each 16 day trajectory where at least 1 fix was recorded per day for at least 15 days of the interval (as a means of removing any trajectories with large gaps that could bias our results). These time-use grids were built across the complete extent of each individuals' relocations during each interval and calculated two statistics: the number of separate visits (nsv) to each cell and the mean locations per separate visit (mlsv) in each cell, which estimate recursion and duration of visit respectively [112]. For this analysis, locations were considered separate visits if more than 12 hours passed between locations within the same grid cell and each grid cell has an area of 1 km^2. This spatial resolution was chosen given the relative temporal coarseness of our relocations and the fact that foraging groups for large herbivores can span large areas.

Overlaying the constructed time-use grids on to the contemporaneous MODIS imagery for each available trajectory, we used R packages `sf` and `velox` [134, 86] to extract the average, median, minimum, maximum, and standard deviation of NDVI values for each 1 km^2 grid cell. We visualized the relationship between nsv, mnlv, and mean NDVI using the `ggplot2` package in R [188].

Annual recursion and home range analysis

To understand how meso-scale rhino movements may translate into home ranges and landscape level spatial-use patterns, we need to examine recursion over a much larger temporal and spatial scale. To begin, we identified 6 individuals within Etosha National Park with consistent fixes for a complete year, from April 2012 to April 2013. Using the same T-LoCoH method as above, we built time use grids for all 6 individuals over the course of their entire trajectories (including fixes beyond the April 2012-2013 interval) identifying separate visits using an inter-visit gap (ivg) of 7 days (as compared to ivg = 12-hr used above). Using a spatial join, we then identified each separate visit within each individuals' time use grids and measured the time to return in days between all visits for all grid cells receiving at least 3 visits within the year. Grid cells including a known watering hole

were removed from this analysis in order to investigate patterns of recursion to presumed foraging sites independent from watering hole use.

As the annual range sizes of our 6 individuals varied widely, we sought to explore how size of range influenced recursion patterns. Are individuals in a constricted range using all parts of their range more frequently than individuals in larger ranges? Are they returning to select areas more or less intensively than their large-range conspecifics? Does range size affect the number of patches, or proportion of an individual's range, an individual uses most intensively? To evaluate these questions, we calculated the mean, median, and standard deviation of the number of separate visits across cells that received at least two visits within the year for each individual. Additionally we calculated the proportion of sites revisited by dividing the number of cells with at least 2 visits by the number of cells with at least 1 visit by the same individual. Finally, we tallied the number of cells for each individual whose number of separate returns was within the top quartile of nsv values observed for that individual. Using Pearson's correlation coefficient, we evaluated the linear relationship between range size (measured as the number of grid cells visited at least once within a year's trajectory) and the mean number of returns to cells, and the standard deviation in number of returns to cells. Additionally we evaluated the relationship between range size and the proportion of cells revisited.

Finally, once again considering all 59 individuals available, to understand how productivity of resources within an individuals' range may inform the size of a range used or needed, we built polygons representing the 90% isopleths of utilization distributions estimated using k-type local convex hull estimation (k-LoCoH), a conservative non-parametric estimator of home range especially good at identifying ranges including hard boundaries or unused areas (e.g., the Etosha Pan) [70, 72]. Isopleths were built on the 16 day intervals identified to align with MODIS imagery for all trajectories including at least one fix per day for 90% of the interval. We then extracted the mean and variance of greenness (viz., greenness=NDVI from MODIS imagery) within each intervals home range using the `velox` and `sf` packages in R [86, 134]. To evaluate the relationship between area and greenness, we fit a generalized linear mixed model using packages `lme4` [14] to handle our unbalanced, longitudinal data, including repeated measures across individuals. AREA measurements were log-transformed before analysis in order to better meet the assumptions of linear regression.

3.4 Results

24 hour displacement cycles

Displacement time-series plots (x-axis, Julian day), for 9 individuals that had consistent 12-hr fixes for at least 30 days, provided some visual evidence for our hypothesized pattern of a series of short displacements followed by occasional large displacements; however, there was little consistency across individuals and no visible pattern across time of year or sex (Fig. 3.3). Across the individual density plots for these individuals, only minor bimodality is seen in some individuals 24-hour displacement (Fig. 3.4).

Investigating 24-hr displacement measures, across 4 different starting times (dawn, midday rest

period, dusk, midnight rest period), revealed that the dawn-to-dawn displacements where on average smaller than displacement measures starting at the other three times of day (midnight, midday, and dusk), which where similar among the themselves (Fig. 3.5). A two sample KS-test between dawn observations and a random sample of measurements from the other three sets of observations (down-sampled to correct for sample size imbalance) rejected the null hypothesis that the samples came from the same underlying distribution ($p = 0.024$). This pattern may indicate that, in general, rhinos are staying within the same area of their home ranges for days at a time, and possibly returning to the same general area days in a row, especially during morning foraging hours.

Investigating the pattern of 24-hour displacement across sexes revealed that, in general, males moved larger distances than did single females or females with calves, but the dusk/dawn pattern held. Investigated across seasons, we would expect that the increased availability of resources in the wet season would erase this effect by reducing the need for long distance movement to find productive resources. As expected, across midnight, midday, and dusk points, more shorter 24 hour movements occurred in the wet than dry season. Twenty-four-hour movement patterns at dawn remained consistent across seasons indicating that dawn-dawn displacement is less water-dependent.

When investigating the time of day of relocation points nearest to watering holes, dusk and midnight had the highest number of relocations found within 0.5 km of a watering hole ($n = 139$ and $n = 138$ respectively). Midday and dawn followed ($n = 109$ and $n = 62$ respectively), supporting previous research that rhinos predominately drink after dusk but also indicating that drinking before dawn is less common. The relationships confirm the importance of the hydration cycle to daily movement with dawn foraging away from water in favoured feeding areas, dusk foraging nearer water and resting site in between.

Biweekly recursion analysis

By splitting trajectories into 16-day intervals and ensuring at least 1 fix per day on 90% of the days, we obtained 480 unique coarse-grained 16-day trajectories, across 48 unique individuals. Time-use grids for each unique 16-day trajectory showed different patterns for those cells that had high recursion rate (high nsv) and those that had long visits (high mlsv) (Fig. 3.6). This likely indicates that features or regions exist that rhinos regularly return to but do not stay long and conversely places where they may not visit frequently but upon arrival stay for extended periods. It's worth noting that while our methods removed intervals with large gaps (> 24 hrs), to maximize the number of individuals included, fixes were not regularized or interpolated before building time-use grids. Therefore, estimates of nsv and mlsv may be underestimated for some intervals and individuals and should be interpreted as estimates of the lower bounds. Across all grid cells used by the 48 individuals and across all intervals ($n = 10733$), the average number of separate visits (nsv) to each grid cell was 1.86 ($\sigma = 1.50$) and the average visit duration (mnlv) was 1.52 ($\sigma = 1.20$ fixes).

Our plot of number of separate visits against mean NDVI extracted for each grid cell visually shows a hill-like relationship with NDVI whereby areas with mid-range NDVI values are most revisited (Fig. 3.7). The duration statistic, mnlv, shows a similar pattern. The mean NDVI of all

cells visited at least once equaled 0.23 ($\bar{x} = 0.23$, $\sigma = 0.12$); Globally, NDVI values of 0.2 to 0.3 generally reflect shrub or grassland ecosystems which is consistent with the study site [186].

Annual recursion and home range analysis

Our investigation of time-to-return between visits on an annual scale showed high variation. Rhinos most commonly returned to sites with high recursion rates (nsv>= 3) within 8-21 days of the last visit; however, across all individuals, some returns occurred months apart (Fig. 3.8), particularly in individuals with larger ranges. Longer times between returns were more common among individuals with larger ranges. When examining recursion across the year, we also found that high levels of recursion were influenced by the size of the overall range of the individual. Two out of six of our investigated individuals had notably constricted ranges; in, at least, one case due to obvious environmental barriers within the range. Range size was also strongly negatively correlated with median number of separate visits ($r = -0.97$) and standard deviation of number of separate visits ($r = -0.85$), indicating a relationship between smaller ranges and higher revisitation to grid cells overall but also support for higher variation among grids cells of smaller ranges. The proportion of revisited cells was also negatively correlated with range size ($r = -0.649$) but appeared skewed by a single point (without SAT280: $n = 5$, $r = -0.96$). Interestingly, the proportion of visited grid cells that had the 25% highest number of separate returns for each individual was fairly stable across all individuals and range sizes ($\bar{x} = 0.22$, $\sigma = .03$). Investigating the relationship between range size and productivity, we found that (log-transformed) area of home range was inversely correlated with mean NDVI values within the short-term ranges (intercept = 16.25±0.19, $\beta = -1.67 \pm 0.54$).

3.5 Discussion

Our results confirm that black rhinos make recursive movements at daily, biweekly, and annual scales; but, for the first time, we have measures for the intensity of these activities among black rhino in northern Namibia and the relationship between recursive movements and spatial resource heterogeneity within rhinos' home ranges. Daily displacement measurements did not strongly support long held assumptions about the potential mesoscale movement of rhinos. Instead they raise new ideas and questions about the daily movement cycle, especially with regards to differences between the dusk-to-dusk and dawn-to-dawn displacement patterns. Our investigation of recursion at the biweekly scale suggests that individuals are returning most frequently to patches with mid-range NDVI values; which, perhaps, is evidence of preference for intermediate shrub environments. We found a strong negative relationship between short-term range size and NDVI indicating that individuals in smaller ranges incorporate higher NDVI on average than individuals with larger range estimates. Recursion to patches across rhino annual home ranges, most often occurred within 2-3 weeks of the last visit, although we also found evidence of seasonal recursions (months apart), particularly in individuals with larger ranges.

Before investigating daily displacement of rhino movement, we hypothesized that daily displacement by individual rhino would produce a bimodal frequency distribution, thereby indicating support for day-to-day movement patterns that include regular short intra-patch movements interspersed with occasional (e.g., weekly or bimonthly) long distance inter-patch movements to new

parts of their larger home ranges. Our results, however, showed only weak support for this hypothesis in some individuals, but no bimodal pattern at a monthly or shorter level. Instead, we found that 24-hour displacement measures have a distinct daily cycle to them, with daily recursion more likely at dawn, whereas dusk-to-dusk and midday and midnight resting cycles produced greater displacement. In contrast to our hypothesis that movements should be more conservative at both dusk and dawn as they are both feeding periods, we found only dawn-to-dawn displacements were conservative.

Rhinos are known to visit waterholes daily to drink, mostly soon after dusk or before dawn. Thus, we also hypothesized that dusk and dawn displacement would be more conservative than resting period displacement. However, in Etosha National Park, where we had coordinates of known watering holes, dawn fixes were among the least likely to be found near watering holes when compared to the other 3 times of day. Also, daily dawn displacement was significantly smaller than at other times of the day. Lastly, comparisons in 24-hour displacement between wet and dry seasons revealed a reduced dusk-to-dusk and midday and midnight displacement suggesting, as expected, that when resources are more plentiful, shorter movements are more viable or attractive. However, dawn-to-dawn displacement was similar among the seasons.

These observations of 24-hour dawn displacement and other times of day in the different seasons inspires new questions and hypotheses about rhino movement. Rhino appear more likely to adopt a recursive strategy to favoured foraging patches in the morning than night-time foraging periods which are more influenced by the need to rehydrate after dusk. The 24-hour displacements we observed may illustrate a trade-off between optimal patch foraging and rehydration where waterholes and favoured forage are distant from each other. Further investigations of the role watering holes and a daily hydration cycle play in daily rhino movements are necessary to obtain a better understanding of this dawn-to-dawn conservative movement phenomenon, especially in cases where complete knowledge of water source locations are available. Furthermore, we suggest that investigating distributions of 24-hour displacement is a useful way of analyzing intermediate-scale movement. In addition, with appropriate interpretation, it is a way to usefully analyse low resolution, gappy animal movement data. Given that much of rhino relocation is commonly gappy and coarse, our approach could help researchers further probe long held intuitions about the way rhino—as well as species such as hippo, with similarly challenging or underutilized data sets—move between and use different areas of their home range.

By investigating biweekly recursions, we were able to link intermediate movement patterns with the finest available temporal resolution for an index of dynamic spatial heterogeneity, NDVI. Our results demonstrate that patch recursion occurs even within as short a time scale as 16 days. Further, the most frequently returned to patches reflect a preference for mid-range NDVI of around 0.25. This range is consistent with global expectations of grassland and shrub ecosystems (higher values would generally correlate with more canopy cover and forest greenness); but, it is interesting to hypothesize why rhinos may select for median rather than maximum available productivity within this system. The intermediate disturbance hypothesis [145] predicts that some moderate level of herbivore feeding provides the spatially and temporally heterogeneous conditions for greater biodiversity and increased productivity of favoured forage. Given this hypothesis, we should expect that rhinos' foraging would spur productivity, which in turn may attract recursion. If such productivity

dynamics are accurately reflected in NDVI, mid-range NDVI patch selection might accurately reflect an intermediate greenness value maintained in the most preferred and hedged browse (like grazing lawns) with the highest rates of recursion. Of course NDVI is only one measure; and, in this case, perhaps an imperfect one. Further study with the aid of LIDAR or other imagery that provides vegetation height and structure data would help to better understand the foraging environments rhinos use intensively.

Interestingly, although home-range size varied among individual rhino, we found that the proportion of grid cells in their range that each frequently revisited did not vary. This would be true if rhino adjusted their range size to include some satisfactory minimum number of feeding patches. In lower quality ranges, patches are sparse and so the range must be larger. In addition, rhino in larger ranges had the longer recursion intervals and lowest recursion frequencies. These patterns are consistent with the idea that feeding patches support more frequent recursion over shorter time frames because they are in more productive habitat. It also supports the idea that rhinos use recursion to engineer productivity in their ranges. Both ideas can be true in a positive feedback between habitat quality and recursive feeding. Further meso-scale rhino movement studies are needed to fully explore these ideas and test whether rhinos are in fact engineering their habitat or just responding to its resources.

An understanding of intra-home-range movement is crucial to bridge existing research at the fine (step-by-step) and macro (home-range) movement scales. By analyzing recursion requiring 7 days between unique visits over an annual cycle, we were able to identify patches within the home range of prolonged, and possibly sustained, value to rhinos over the course of the year. Our results offered new insight into how range size may affect resource use within an animal's range long term, an especially relevant topic given that the surviving populations of rhinos are often in small, fenced, and sometimes isolated reserves or ranges. Our analysis of grid cells with known watering holes provided evidence that these cells often received a very high frequency of separate visits with low average duration at a 7-day inter-visit-gap resolution, although our sample size was too small for this evidence to be definitive. Additionally, though our analysis included all known watering holes within the park, it is likely that some seasonally available, or small, unmarked waterholes went unidentified. Our results suggest, however, that our scale of recursion analysis can become an effective tool for identifying locations of previously unknown watering holes. Future analysis is needed to investigate how long-term recursion patterns and time to return track directly with productivity and may change in the wet versus dry season. If recursion is driven by resources and productivity, one might hypothesize given the increased resource availability and productivity during wet seasons that time to return would be significantly shorter than during the dry season where biomass regeneration is slowed.

3.6 Conclusions

These results are a rare glimpse into meso-scale movement patterns of the black rhinoceros across a majority of its remaining range in Namibia. The black rhino population sampled here is the third largest in Africa and the only viable population of *Diceros bicornis bicornis*. The endemism of this unique sub-species and the rhinos' unique adaptation to the arid habitat in the west makes

it all the more crucial to conserve. However, the impact on global biodiversity of conserving the black rhino goes well beyond the conservation value of a single species. Globally, megaherbivores ($>$ 1000 kg [131]) support an extraordinary amount of biodiversity as ecosystem engineers. Through their feeding behavior and long distance migration and dispersal, megaherbivores maintain open landscapes by reducing tree cover, transport seeds and nutrients, and significantly influence the species composition and carbon storage in the ecosystems they inhabit [122, 53, 19, 182, 38]. A better understanding of their recursive movement patterns, particularly at the meso-scale, is crucial for understanding and conserving this species and the unique ecosystems they help fashion.

3.7 Figures

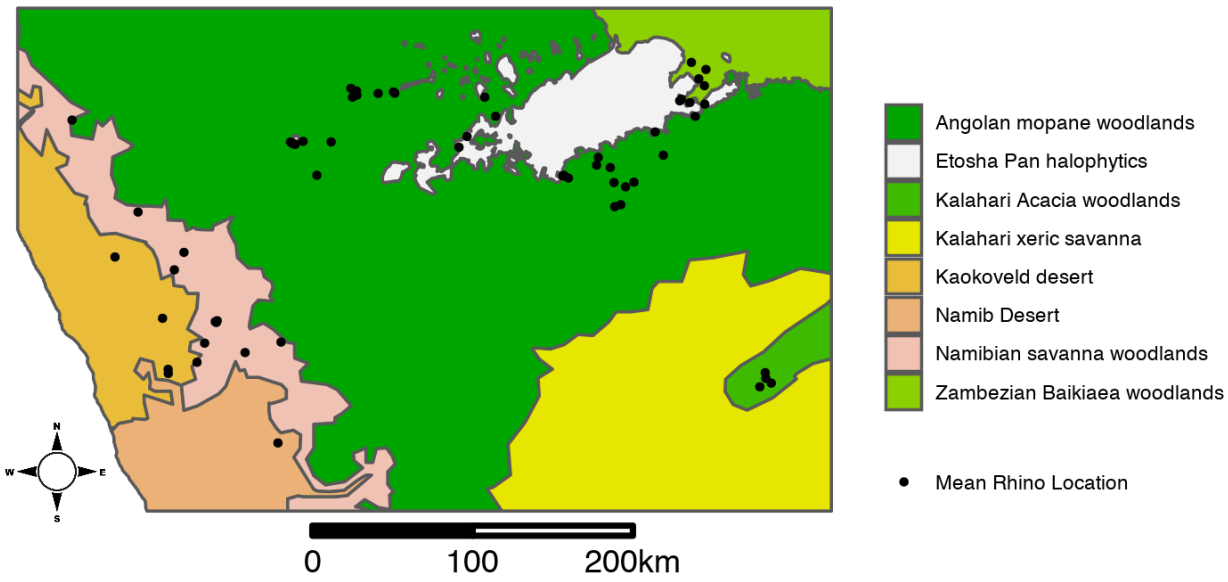

Figure 3.1: **Study area map.** Distribution of geo-tagged individuals across Namibian ecoregions as specified by Dinerstein et al. [48].

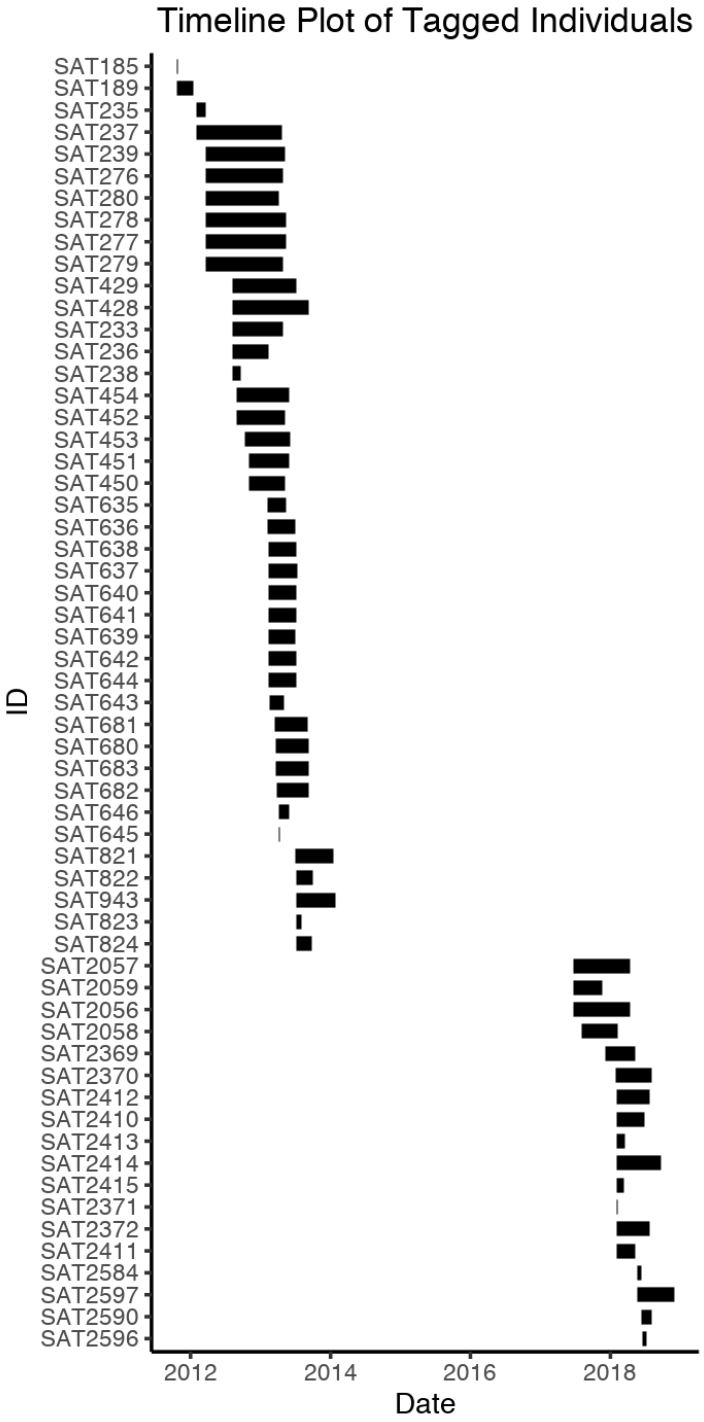

Figure 3.2: **Timeline plot of individual sampling regimes.** Timeline plot indicating sampling intervals for all individuals used in the study. Produced using R package `stmove` [150].

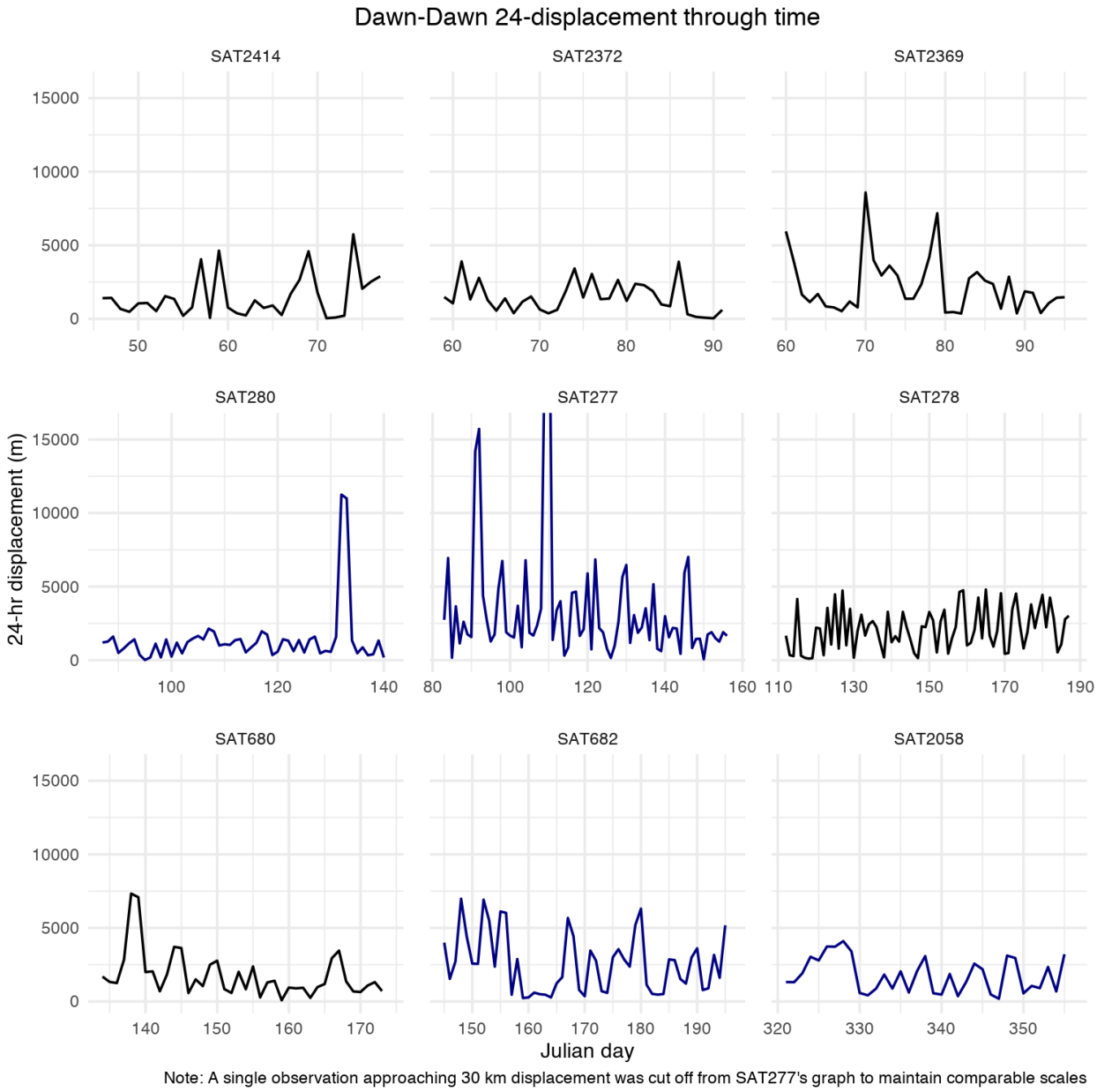

Figure 3.3: **Twenty-four-hour displacement time series for individuals with consecutive fixes** Dark blue represents males. Note that plots are arranged so that Julian dates get larger right to left and down the columns to aid the reader in evaluating seasonal trends.

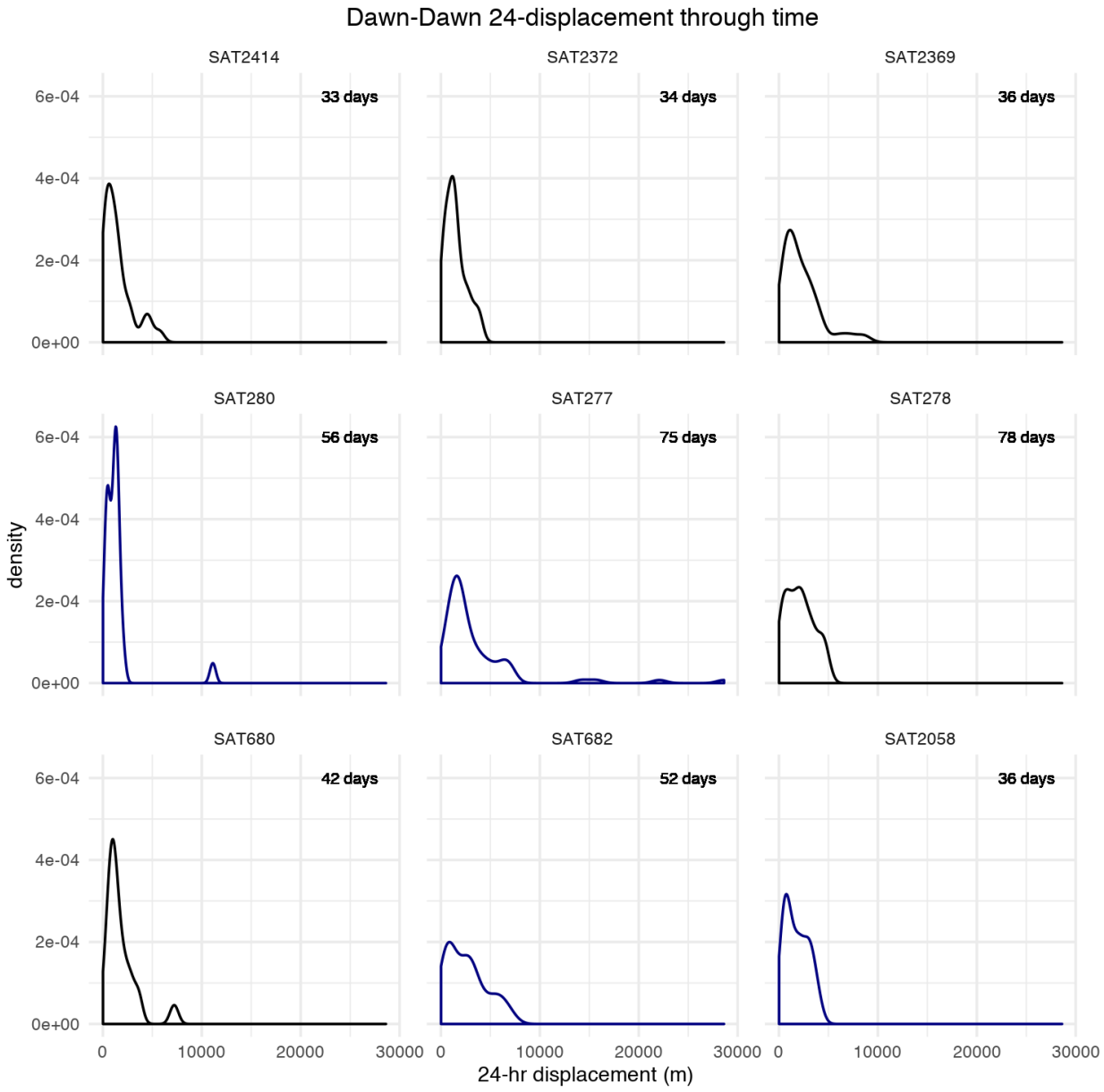

Figure 3.4: **Density plots of 24-hour displacement across consistent individuals** The order of plots reflects that in Fig. 3.3 and the dark blue again indicates male rhinos. The bimodality in some plots offers weak support for the notion of short movements interspersed with occasional long movements within and between areas of the home range.

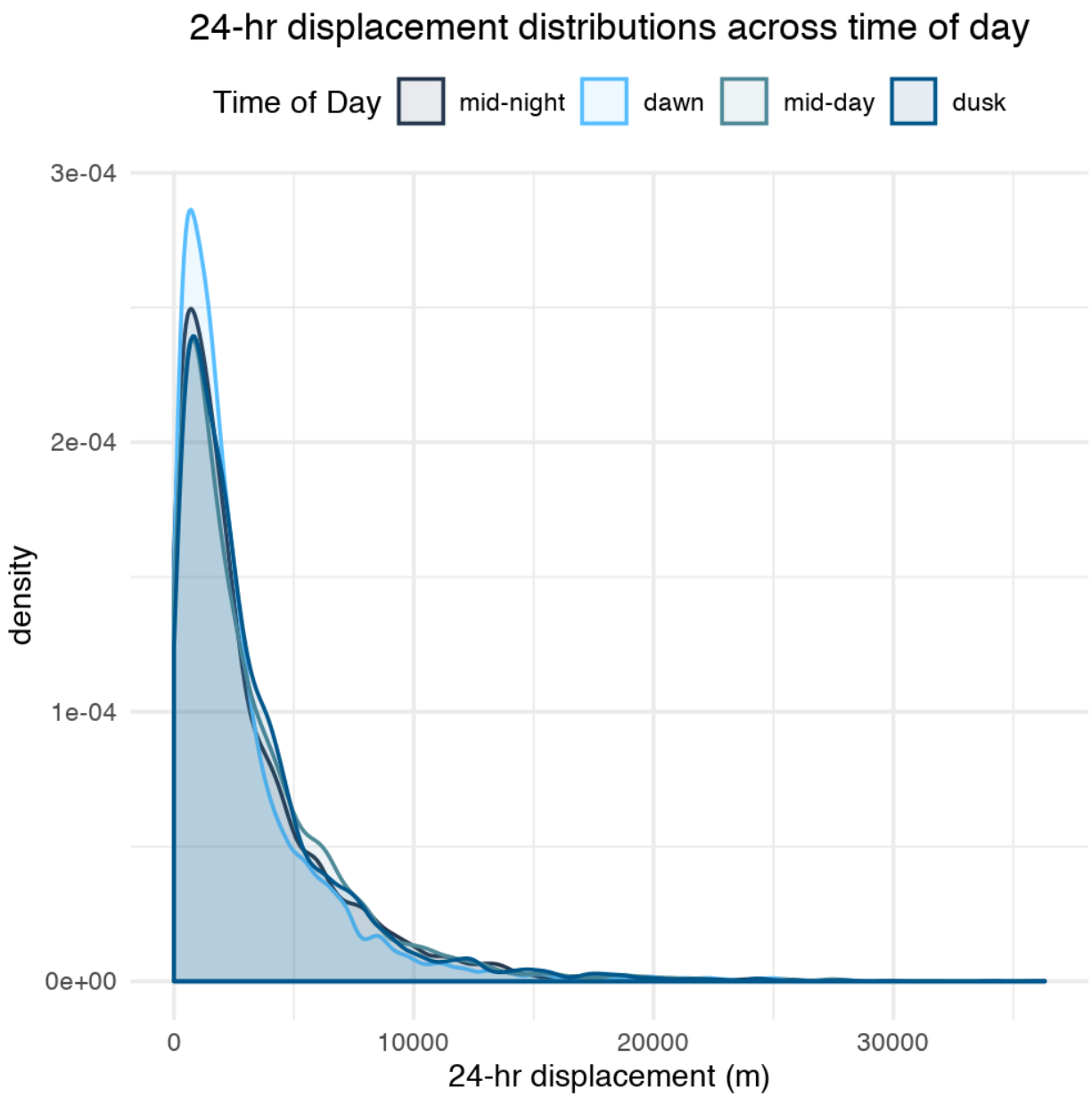

Figure 3.5: **Density plots of 24-hour displacement across 4 regularly spaced diurnal starting times**. Dawn-to-dawn times are significantly different from the other three ($p < 0.024$ see text for details), driven by a higher frequency of shorter displacements.

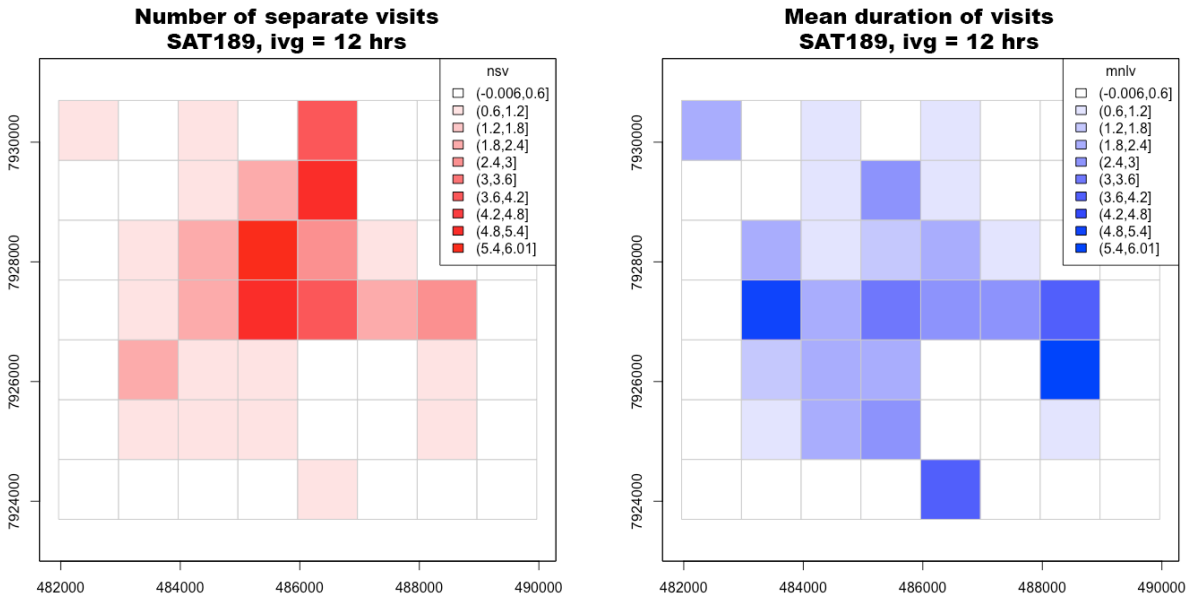

Figure 3.6: **Example time-use grid plots, rhino SAT189.** Side-by-side plots illustrate two time-use metrics for a single 16-day interval for individual SAT189. Left panel: the number of separate visits (nsv) to each grid cell (1 km^2 areas with an intervisit gap of 12 hours apart). Right panel: the mean number of locations per visit (mnlv) to each grid cell.

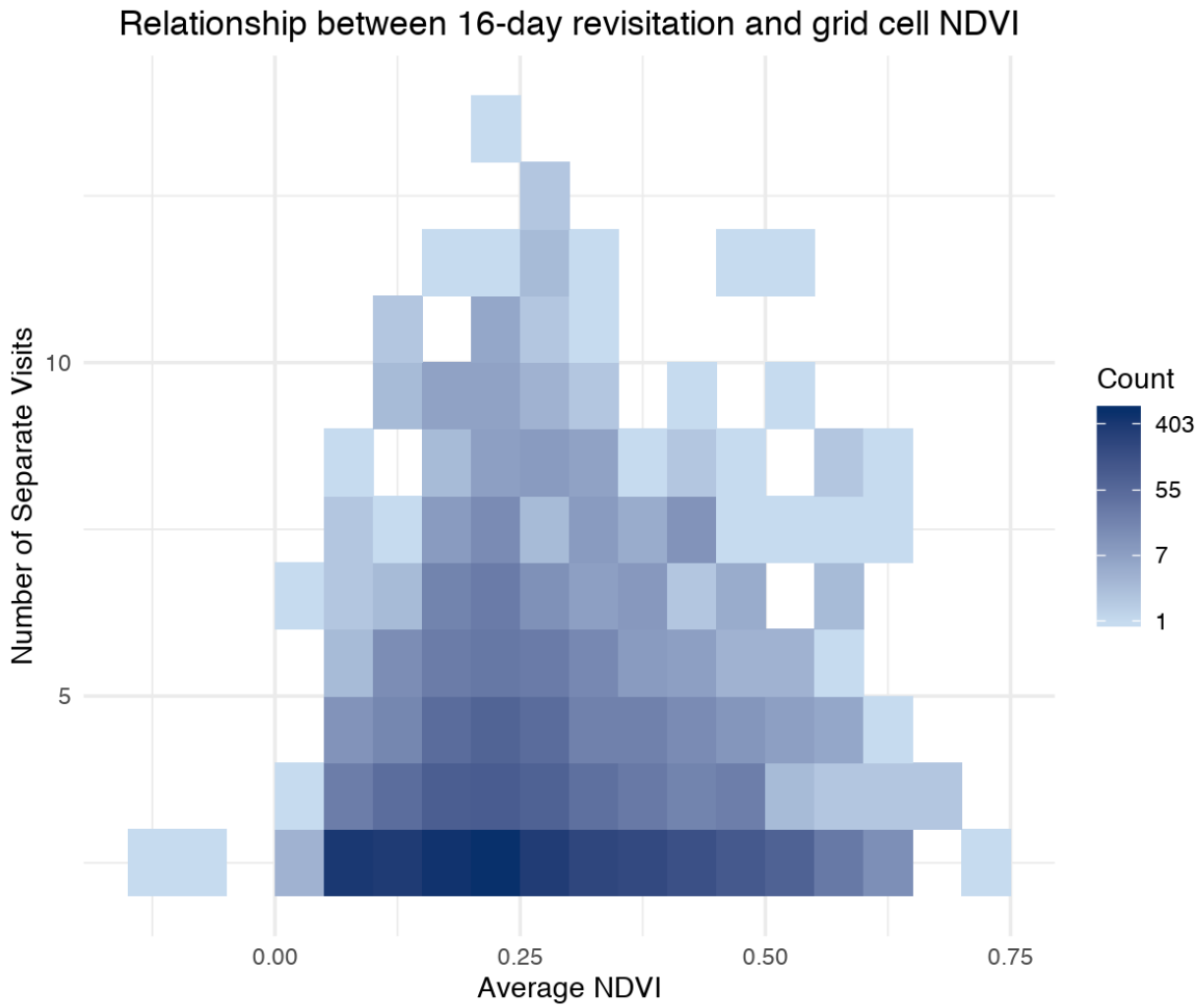

Figure 3.7: **Relationship between 16-day revisitation and grid cell NDVI.** A heat map showing the density of points along axes of number of separate points and mean NDVI values. The color scale is log transformed to better visualize the variability at the lower end of the nsv measure. Note that the highest density of grid cells have 2 visits and a mean NDVI of ≈ 0.25. This plot does not include grid cells not visited or returned to, i.e. nsv < 2.

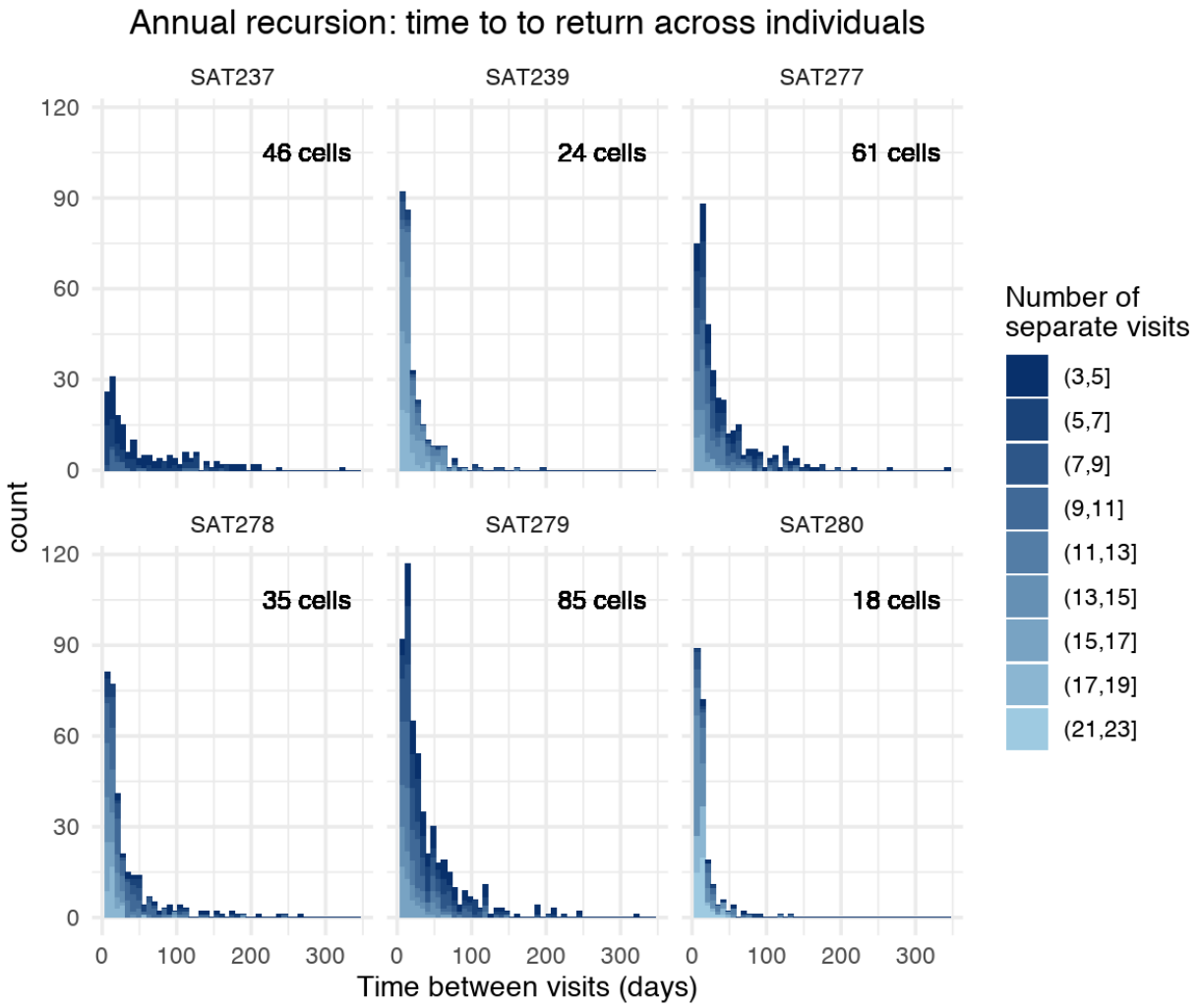

Figure 3.8: **Annual recursion: time to return across individuals**. Side-by-side histograms display the distribution of time between visits to grid cells for each individual. The bin width of each bar is 7 days. Lighter colors indicate returns to grid cells with higher numbers of returns. The number of visited grid cells in each individuals range is included in the top-right corner of each plot to highlight the variability in recursion patterns correlated with range size. Across all individuals the most common time to return is within 8-21 days (the first 2 weeks), but all individuals see at least some returns months apart. Individuals with smaller ranges tend to have higher rates of return and shorter times between returns. Individuals with larger ranges, have much longer tails of their distributions potentially showing support for seasonal returns to different areas of their home ranges.

Chapter 4

Exploratory movement analysis and report building with R package `stmove`

Dana Paige Seidel Eric R. Dougherty Wayne M. Getz

4.1 Abstract

Background As GPS tags and data loggers have become lighter, cheaper, and longer-lasting, there has been a growing influx of data on animal movement. Simultaneously, methods of analyses and software to apply such methods to movement data have expanded dramatically. Even so, for many interdisciplinary researchers and managers without familiarity with the field of movement ecology and the open-source tools that have been developed, the analysis of movement data has remained an overwhelming challenge.

Description Here we present `stmove`, an R package designed to take individual relocation data and generate a visually rich report containing a set of preliminary results that ecologists and managers can use to guide further exploration of their data. Not only does this package make report building and exploratory data analysis (EDA) simple for users who may not be familiar with the extent of available analytical tools, but it sets forth a framework of best practice analyses, which offers a common starting point for the interpretation of terrestrial movement data.

Results Using data from African elephants (*Loxodonta africana*) collected in southern Africa, we demonstrate `stmove`'s report building function through the main analyses included: path visualization, primary statistic calculation, summary in space and time, and space-use construction.

Conclusions The `stmove` package provides consistency and increased accessibility to managers and researchers who are interested in movement analysis but who may be unfamiliar with the full scope of movement packages and analytical tools. If widely adopted, the package will promote comparability of results across movement ecology studies.

4.2 Background

With the increased accessibility of GPS data and expanded computing power for analyzing such data, a concomitant open-source software expansion has occurred for exploring spatiotemporal structure in movement trajectories. With this expansion of data and tools, two vexing problems remain for researchers and managers: 1.) lack of a unifying movement-pathway framework that would facilitate comparisons across studies; and, 2.) lack of software-package accessibility (e.g., using R or Matlab) to those not steeped in movement ecology or those lacking proficiency in command line program implementation.

These two problems are exacerbated by the sheer volume of available tools, which has resulted in an overwhelming landscape of analytical options. This is especially challenging for researchers or managers who fortuitously get access to GPS relocation data, but have little or no experience in analyzing movement trajectories. R has emerged as an open source programming platform of choice for movement ecologists, primarily because of the large number of statistical and data manipulation packages that have become available to aid researchers in conducting even the most obscure domain-specific analyses. In a recent review of R packages solely dedicated to movement or tracking analyses, 57 individual packages were listed, with only 12 having good to excellent documentation [92]. It is also clear that, while these open-source, programming languages—with R being a primary example—have made it possible for scientists to carry out an ever-growing list of new and developing analyses, these packages constitute a variety of different, and not all together compatible, methods and data structures. Thus, this burgeoning cornucopia of tools can be as much a stumbling block as a godsend for many researchers and managers: even with access to a trove of GPS movement data, they may not have the time or expertise to assimilate which of the available toolkits is most appropriate for their analytical needs.

Building on the work of previous open source contributors, our `stmove` R package alleviates the first of these problems—i.e., lack of a coherent framework—by setting forth a standard set of first-pass exploratory analytical methods that should be performed before undertaking more specific or targeted movement analyses. Further, it mitigates the barrier-to-use problem by conveniently gathering in one place a disparate set of compatible tools and methodologies and providing a single command (and optionally interactive) infrastructure for automated report building that can run analyses and compile results into a digestible, visually rich report. From this report, researchers and managers can then distill key insights needed to sharpen current interpretation and subsequent exploration of their movement data. Of course, our package cannot streamline research to the point where no additional analyses are needed: many questions require deep methods that are too sophisticated to be included in a general entry-level R package. Instead, our package seeks to make it much easier to carry out a first cut analysis, using a standard set of methods. We propose that such analyses, as detailed in the implementation section, should to be undertaken before more powerful methods, required to address complex questions, are applied.

4.3 Implementation

R is an open source and system-agnostic language [143], with a growing user base in the ecology and environmental science communities. Our `stmove` package can be used on any computer with R installed regardless of operating system (e.g., MacOS, Linux, or Windows). Alternatively, `stmove` may be used within a web browser when combined with external cloud computing services such as RStudio Cloud. The primary goal of `stmove` is to preform a standard set of exploratory data analyses and return a preliminary report with visualizations, interpretation aids, and suggested next steps to empower managers or researchers new to movement analysis. In addition, it aims to give all users a simple work-flow of best practice analyses from which to begin any movement study. Although all analyses are standalone and can be preformed separately on individual trajectory data, the primary advantage of this package is its report building function that conducts multiple analyses and provides a PDF report for each inputted set of movement trajectory data. This report includes 4 central components: general distributions (step-size and turning angles [123]), interval statistics (means, variances, auto and cross-correlations, and plots of running averages of these), wavelet analyses [191, 140], and home-range constructions [70, 193]. Additionally, `stmove` functions to summarize multiple trajectories in space and time. Each of the packages main components and their underlying methods are discussed below. Software design choices have been made to further simplify the use of `stmove`, including sensible defaults and an interactive HTML add-in to help guide report building for users implementing `stmove` within the popular RStudio IDE (integrated development environment).

Individual analysis

The goal of `stmove` is to make more accessible the standard spatiotemporal approaches to analyzing and interpreting movement data before implementing project-specific approaches to deconstructing movement trajectories. Application of `stmove` requires a *clean, regular, GPS time series of relocation data* consisting of a sequence of $T+1$ points (x_t, y_t, t) where $t = 0, 1, 2, 3, ..., T$, and all missing points have been interpolated and filled in. Additionally, locations (x_t, y_t) are expected to be in a projected coordinate system—the unit of measure in the coordinate system determining the unit of measure for calculating the step-size (s_t) and turning-angle (θ_t) time series of lengths T and $T-1$ respectively [123], using the equations

$$\begin{aligned} s_t &= \sqrt{x_t^2 + y_t^2} \\ a_t &= \arctan\left(\frac{y_t - y_{t-1}}{x_t - x_{t-1}}\right) \\ &\quad - \arctan\left(\frac{y_{t-1} - y_{t-2}}{x_{t-1} - x_{t-2}}\right) \end{aligned} \tag{4.1}$$

All analyses are intended to be performed on a single individual's trajectory to provide insight on individual movement patterns; see our population analysis section to review the analyses available for multi-animal datasets supported by `stmove`.

Regularization and Interpolation

Ensuring that relocation data are complete and regular—that is, the data collection frequency must be fixed and no values should be missing—can represent a sufficiently challenging hurdle to movement analyses that it may be the reason why GPS data often go unanalysed. Even for telemetry data collected at a set fixed rate, relocation timestamps can be imprecise, recorded within a few seconds or even minutes of the scheduled time, due to lags in satellite connections, and fixes may be missed altogether for a variety of reasons.

To help researchers easily regularize near-regular data, the popular `adehabitatLT` R package [29] has two functions 'setT0' and 'setNA' which `stmove` has wrapped together in a new function called 'regularize' to help users easily regularize their data. Given a reference date and time and an expected fix rate, 'regularize' will round fix times to the nearest fix (within a set tolerance) and insert NAs (formal missing value notation) for all missing values to build a regular time series. Because further analyses require complete trajectories, `stmove` then provides the function 'kalman' for interpolation of missing values.

The 'kalman' function uses Kalman smoothing to interpolate missing values in the x and y coordinates of a trajectory. The Kalman smoothing approach is a state-space model that uses all available observations (rather than just the past and current observations, as in the case of Kalman filtering) to derive the covariance structure of the data and predict the current state. This function, based upon the 'na.kalman', 'StructTS', and 'auto.arima' functions of the `imputeTS` package [124], selects the best fit structural (linear, Gaussian) time-series model for each univariate time series in turn—i.e., treating the series x_t and y_t separately—and then applies Kalman smoothing (based upon the chosen best fit models) to iteratively interpolate any missing values. Since our intention is to provide a rapid, flexible way to interpolate missing points for the purposes of exploratory data analysis, `stmove`'s 'kalman' function is optimized for rapid estimation rather then the most accurate possible interpolations. For this reason `stmove`'s 'kalman' implementation reports the ratio of interpolated to empirical points and issues a warning to users when interpolating more than 5% of a trajectory's total points. Because errors associated with interpolation degrade the accuracy of ensuing visualizations and analyses knowledge of this ratio forms part of an assessment (albeit informal) of the reliability of the results obtained. If users are seeking to analyze trajectories with large gaps between otherwise consistent fix intervals, they are encouraged to break trajectories up into sub-individual trajectories or choose the largest continuous section of sampling for subsequent analysis rather than interpolating over large gaps. For intentionally gappy or opportunistically gathered telemetry data (e.g., from marine mammals when surfacing, or from older or failing satellite collars), more rigorous models for interpolation may need to be considered. These methods, however, are outside the scope of the `stmove` package and are discussed elsewhere [133, 90, 108].

Visualizations and Distributions

Before undertaking any exploratory data analysis, it is generally helpful to visualize the data. In the case of movement data, visualization of a trajectory can show outliers, recursions [11, 18] and syndromic movement behaviors [2], and the individual's general space use pattern. Implemented using R's `ggplot2` package [188], the first plot returned by `stmove`'s 'build_report' function is

a simple scatter plot of the (x, y) coordinates of all locations defining a given trajectory (e.g., see Fig. 4.4). The next plots in the report are histograms of step size s_t and turning angle a_t. These are obtained by `stmove` converting a user-provided dataframe of relocations to an 'ltraj' object (an object class defined by the popular `adehabitatLT` package [29]) and then calculating the step-size and turning-angle time series using Equations 4.1 (e.g., Fig. 4.5). `stmove` then plots step-size and turn-angle histograms using `ggplot2` (e.g., see Fig. 4.5; [188]). From these plots depicting the frequency of different step sizes or turning angles, users can begin to identify outliers and perhaps detect behavioral modes or directional biases in the trajectory.

Rolling Statistics Our next step is to calculate the primary times series statistics using rolling (sliding) windows $W(t, w)$ of a given fixed length w and starting at time t. Within windows $W(t, w)$ for $t = 0, ..., T - w$, `stmove`'s 'rolling_stats' function computes running step-size and turning-angle means, as well as single-lag autocorrelations and cross-correlations of the s_t and a_t time series. These rolling windows are implemented using `RcppRoll`'s 'roll_meanr' and 'roll_sdr', and `TTR`'s 'RunCor' functions [175, 174], all statistics are calculated with a right-aligned window. If fix rate is sub-hourly, the rolling window defaults to three hours, if the fix-rate is one hour or more, the window is increased to six hours. These defaults can be overridden with the optional 'n_roll' parameter allowing users to specify how many fixes they wish to "roll" over when calculating statistics. This argument is particularly powerful if users are investigating a trajectory with a large fix rate (i.e., $>$ 3 hrs), for which the default behavior will not provide especially informative results. Rolling statistics are often used as inputs to more advanced types of movement analyses [56, 151]. These rolling window plots offer users insights into behavioral patterns that may relate to the identification of different modes of activity (e.g., using break-point analyses [79, 80]). In addition, we note that auto- and cross-correlations are transformations of primary movement metrics that can estimate persistence in either direction (acf_ang) or distance/speed (acf_dist).

Interval Statistics While rolling statistics can smooth patterns through time, interval statistics are a preliminary means to identify patterns across discrete, biologically meaningful periods of time. `stmove`'s 'interval_stats' function can be used to calculate the mean and variance of a trajectory's primary movement statistics across three intervals of interest: diurnal, lunar, and seasonal. Diurnal analysis summarizes these statistics for 12 hour windows representing pre-noon (0-12) and post-noon (12-24) hours, as determined by the time zone associated with user-inputted data. Lunar interval analysis relies on the `lunar` package [101], automatically dividing a given trajectory according to periods within the lunar cycle, full-waning, and new-waxing intervals according to date. Seasonal interval analysis is customizable with `stmove`: 'interval_stats' recognizes an optional 'seas' argument by which users provide a character vector of season start dates. In this way, users are allowed to specify custom seasons over which to calculate the interval statistics. Which interval statistic is appropriate may depend upon the length of a users trajectory and/or the biology of the tracked animal. As such, when building a report, the user can specify which interval statistics they would like to include using the 'stats' argument.

Wavelet transform and visualizations

Many factors influencing movement are cyclic with periods that are linked to ecological relevant frequencies (e.g., regular resource gathering trips, migration, or certain social and reproductive behaviors). Fourier and wavelet transformation methods are useful analyses to examine the cyclical nature of animal movement and behavior [191, 140]. Especially as a part of exploratory analyses, these time-frequency methods are useful for understanding dynamic movement responses to physiological, ecological, climatic, and landscape factors [191, 140]. After `stmove` has calculated basic path distributions and statistics, it implements a wavelets analysis on user-selected time series, using Morelet filters, by importing functions from an existing open source R package, `dplR` [24, 25]. The user-selected time series are step sizes, turning angles, autocorrelation coefficients of both coefficients and their cross-correlation coefficient. It then produces a plot of the local wavelet power spectrum that users can then use to visually identify any possible periodic components (e.g., see Fig. 4.7).

Basic space constructions

A crucial step to exploring movement data is understanding what a given trajectory can tell us about higher order space use, notably an animal's core area or home range [193]. There has been considerable debate regarding the best tools for evaluating landscape level space use, including methods from minimum convex polygons that are conceptually simple and computationally cheap to more complex methods incorporating an animals probability of occurring in a given location [62]. `stmove` incorporates two non-parametric spatial construction methods for users to choose among when estimating 25, 50 and 95% home range isopleths: a Local Convex Hull construction implemented with the `tlocoh` package and an auto-correlated utilization distribution analysis implemented with the 'akde' function from the `ctmm` package [70, 113, 28, 64] (e.g., see Fig. 4.8). Both methods have their particular strengths: the `ctmm` AKDE method (i.e., implemented using the 'akde' function) provides a statistically rigorous construction when analysing correlated data under the assumption that movement is an Ornstein-Uhlenbeck process—i.e., a continuous time generalization of an autocorrelated random walk, sometimes with drift added [28, 128]; and, when the latter assumption is not valid (e.g., when the frequency of relocation sampling is at the same or longer time scales for which movement decisions are influenced by environmental factors) `tlocoh` implicitly accounts for vegetation and landscape structures, as well as hard boundaries due to irregular landscape features [70, 72, 112]. In `stmove` we implement k-LoCoH with $k = \sqrt{n}$ (rounded to the nearest integer, where n equals the number of relocations in the time series). We also note that the `ctmm` 'akde' method produces space-use estimates with confidence intervals that appropriately account for the autocorrelation inherent in movement data. Either method can be implemented using the 'construct' function and specifying the method with the 'type' argument.

Population analysis

Though the package is designed to build reports for individual trajectories, when provided with a data frame storing multiple trajectories specified by four columns—x, y, date, and id—`stmove` is able to create an additional cover sheet showing spatial and temporal overlap of the individuals in the dataset using two important functions: 'plot_timeline' and 'dist_map'. These plots, built

using `ggplot2` [188], summarize the spatial and temporal overlap of trajectories. In the first plot, a segment graph produced by 'plot_timeline' is displayed, with lines identifying the duration of time sampled for each individual in the data frame. In the second plot, built by 'dist_map', all of the included trajectories are plotted with a single point representing the mean x and y coordinate over the course of the full path and colored according to the mean year of sampling. These visualizations provide a straightforward summary of the spatial and temporal spread of trajectories within a data set (see Figs.4.2, 4.3).

Report Building

The primary product of this package is 'build_report', which produces a PDF report of the results of the analyses described above, when given a clean, regularized trajectory. Beyond the initial three plots discussed in the *Visualizations and Distributions* subsection, which are included in all reports, reports can be customized to include any or all of the analyses by changing the arguments passed to 'build_report'. 'build_report' is implemented using the `rmarkdown` package [7, 195] and parameterized templates that are distributed and installed with the package. The templates use the popular visualization package `ggplot2` [188] to deliver users a report with custom visualizations of their selected analyses. To aid users in customizing their reports, we have implemented an interactive HTML widget that can help guide users of the popular IDE RStudio in building their own movement reports (Fig. 4.1).

4.4 Illustrative Example

We illustrate the implementation of the `stmove` package using relocation data collected from a population of African Elephants (*Loxodonta africana*) in and around Etosha National Park, Namibia. We generate our `stmove` analyses and report using a data frame containing 15 individual trajectories previously published by Tsalyuk et al. [171]. After initial regularization, each individual trajectory contained between 5633 to 113652 empirical relocations. This unique data set contains individuals tagged from October 2008 through July 2015 for variable-length sampling periods and fixed rates.

Population Analyses

For data sets with multiple trajectories, the `stmove` population functions provide a powerful summary of our complete data set in a population level "cover page". The 'plot_timeline' function produces Fig. 4.2, a plot that immediately captures the coverage of and variability in sampling intervals across the population. In a second plot, produced by the 'dist_plot' function, Fig. 4.3, the spatial and temporal distribution of individuals is displayed by plotting for each individual its the mean location $(\bar{x}, \bar{y})$ from all fixes available. Each mean x-y point is then colored according to the average year of the relocations. These abstractions distill 724,925 points and 15 individuals concisely to communicate the spatial and temporal spread of our population. From these plots we see that we a group of one individual on the eastern end of our space, a group of four in the center top and a string individuals in the eastern bottom half of our space. have at least one group of individ-

uals clustered very close together, perhaps because of habitat constriction, opportunistic sampling, or social structure. This sort of result immediately spurs questions for further analysis, including those concerning the social structure of our population of interest, exemplifying the purpose of solid exploratory data analyses and the `stmove` package.

Data regularization

To demonstrate the per-individual metrics of the package, we use data from individual AG195, a female elephant collared from July 2009 through September 2011 with fixes taken at consistent but irregular intervals, with points collected in repeating intervals of 1 minute and 19 minutes. Before analysis with `stmove`, regularization was performed using 'regularize' and an expected fix rate of 20 minutes – eliminating every other fix in order to standardize the interval to 20 minutes for future analysis (50% observation loss). The complete regularized trajectory consisted of 55,524 relocations but for ease of demonstration and interpretation we will use only relocations from 2010 in the following analyses ($n = 26277$). This regularization procedure was followed by the execution of the 'kalman' function to interpolate 3 missing fixes along the trajectory, 0.01% of the total path. At this point, AG195's clean, regular, and complete trajectory ($n = 26280$) is ready for analysis with `stmove`.

Individual Metrics

Running 'build_report' with our complete, and regular trajectory for AG195, three plots are provided to begin: an x-y plot of the path (Fig. 4.4) and two histograms (Fig. 4.5) showing the distribution of step sizes (meters) and the distribution of turning angles (radians). Investigating these plots, we easily identify the range and most common step sizes of this elephant, based on a sampling interval of 20 mins: it most commonly moves less than 100 meters; but, on rare occasions, it moves upwards of a kilometer in this time interval. From the empirical distribution of turning angles we see that individual AG195 does not have a preferred turn direction and, from the strong peak in the histogram around 0 radians, some correlation is evident in directional persistence over periods that exceed 20 minutes. These empirical distributions are useful for identifying general behavioral profiles or outliers. Additionally, it is common to sample from these same empirical distributions when simulating movement tracks for future analyses.

In a `stmove` report that includes rolling statistics, three plots are provided of the running values for mean_dist, mean_ang, acf_dist, acf_ang, and ccf. Plots of mean_dist and mean_ang are, by default, faceted by month to handled long term datasets with high resolution. The third plot displays smoothed conditional means splines across all rolled values of acf_dist, acf_ang, and ccf to give a high level view of patterns in these statistics across the entire temporal extent of the trajectory. Note in Fig. 4.6, the clear increase in mean step size in the months of February and March 2010, possibly the marker of increased movement during the start of the wet season. Diurnal interval statistics are plotted in similar fashion, with separate splines for morning versus evening intervals to illuminate differences between them. Coarser intervals, i.e. lunar or seasonal, are plotted using stair-step plots or bar charts to clearly demonstrate how estimates change from one interval to the next (Table 4.1).

When wavelet analyses are included within a report they can be applied to any of the 5 primary statistics and return individual power spectrum plots (Fig. 4.7). As an exploratory data analysis tool, these plots are intended to illuminate periodicity in the trajectory if it is present; for more information on wavelet transformations and the interpretation of these plots, we direct readers to Torrence and Combo's practical guide to wavelet analysis [169]. Also, for examples of interpreting wavelet plots in movement ecology see [191, 140].

Finally, our full report for AG195 includes two methods of home range construction: a k-LoCoH hull set and an auto-correlated kernel density estimation both plotted with 25, 50 and 90% isopleths (Fig. 4.8). The methods differ profoundly and produce notably different estimations of space use with k-LoCoH often being quite restrictive and AKDE offering larger estimates with confidence bands. LoCoH methods provide clear information of where the animals have been and the areas locally bounded by the relocation points, while AKDE provides projections of where the animal is likely to be found if environmental and landscape features do not play a role in the animals movement behavior.

A final note of caution for users, although we have demonstrated a report including examples from all possible analyses here, which analyses are relevant to study at hand will be dependent on many variables including animal behavior, sampling rate and sampling duration—and, of course, questions of interest. Although animal movement is inherently a continuous process, relocation sampling is a discrete process in space and time. The sampling resolution influences the analyses and the conclusions one is able to draw regarding animal movement behavior [36]. Therefore, consideration of the resolution of your data is crucial before deciding which statistics to include in your custom report. Rolling and diurnal statistics, as well as wavelet plots, often are more appropriate for trajectories with higher resolution data. Interval statistics at the lunar or seasonal level are appropriate for larger-grain data, provided that sampling continued for long enough. Both home-range construction options can be used on data at any resolution, although AKDE is more appropriate at relatively high temporal resolution (on the order of minutes and fractions thereof) while LoCoH methods are appropriate and lower levels of temporal resolution (hours and large fractions thereof). We encourage users to think critically about the nature of their data before conducting even the most basic exploratory data analyses.

4.5 Conclusions

In 2008, Ran Nathan *et al.* [126] laid out the movement ecology paradigm, which effectively situated the emerging discipline within the broader ecological context, but fell short of dictating a set of baseline analyses that should be run on any newly-collected movement data. The movement ecology paradigm has informed the hypothesis generation process and guided the data collection procedures of innumerable studies, but the absence of a core set of standardized analyses among the many novel tools available to researchers has made it difficult to contextualize the movement patterns of an animal or species and to compare across studies and wildlife. `stmove` strives to fill the gap and make it easy for researchers to employ a standardized set of tools that provide basic insights into the movement of individuals. While this package is primarily an opinionated wrapper around other open-source contributors' work and packages, the primary advantage and goal of this package is

to provide a simple, single-command procedure to produce comprehensible and customized reports covering important baseline analyses one should conduct on GPS movement data. Once these analyses have been undertaken and properly interpreted, one can then pursue various kinds of analysis that address subsequent questions of interest (e.g., generalized linear models of location and landscape [116], hidden Markov modeling to identify behavioral states [132, 120], or step selection analyses [164, 10]). This package strives to set a standard for what is minimally needed before embarking on such analyses and in doing so hopes to provide a framework and infrastructure that democratizes foundational movement analysis and enhances comparability of studies.

4.6 Tables

Table 4.1: Interval Statistics. An example of Lunar statistical output (AG195)

interval_start	phase	mean_dist	sd_dist	acf_dist	mean_ang	sd_ang	acf_ang	ccf
[1,12)	Full-Waning	99.827	125.683	0.571	-0.001	1.313	-0.035	0.028
[12,26)	New-Waxing	117.765	122.113	0.517	0.015	1.217	-0.061	-0.012
[26,41)	Full-Waning	180.998	238.705	0.686	-0.036	1.317	0.020	0.041
[41,56)	New-Waxing	244.072	284.247	0.710	0.064	1.300	0.023	-0.026
[56,71)	Full-Waning	210.297	253.647	0.674	0.065	1.366	0.043	-0.018

4.7 Figures

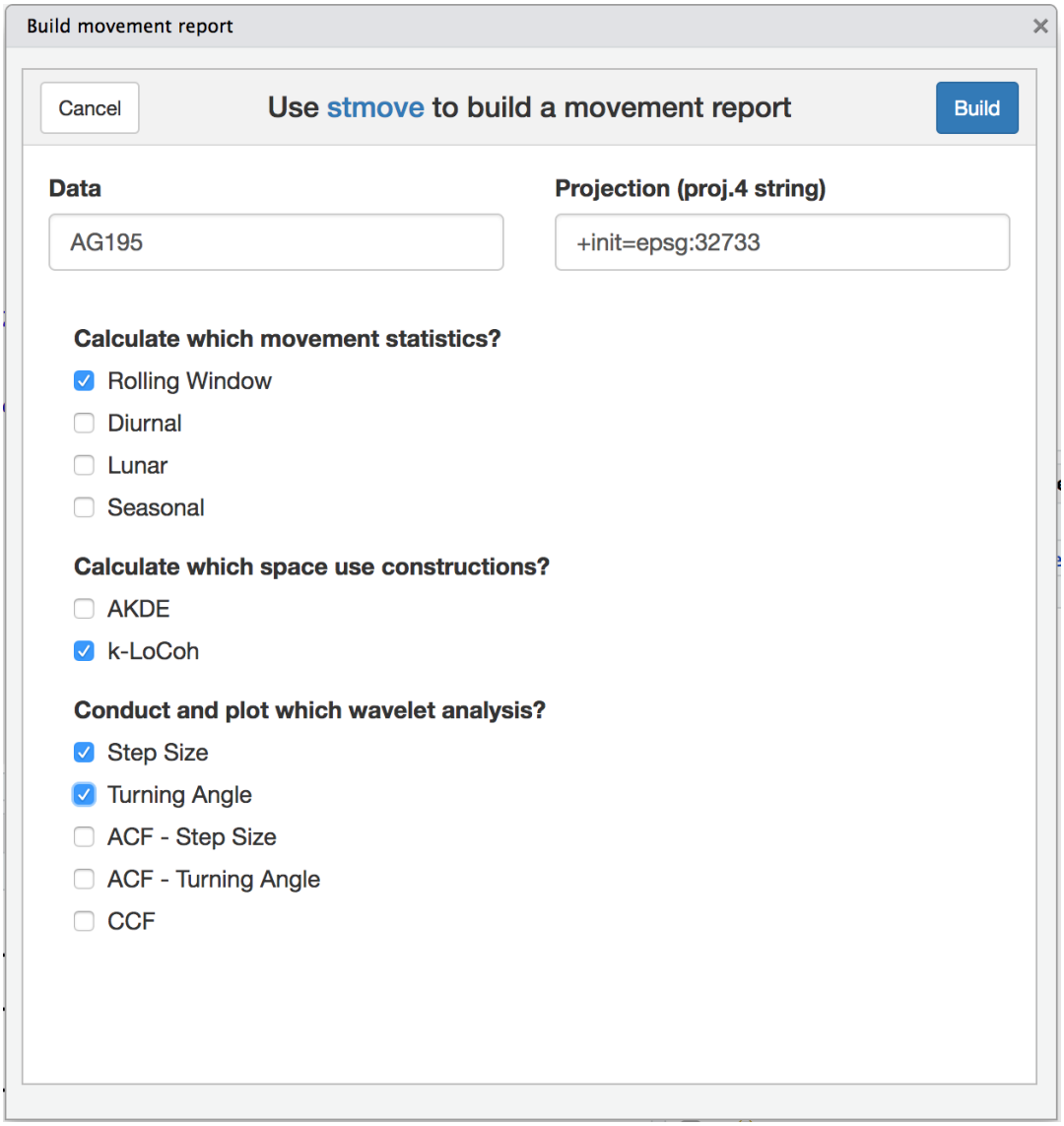

Figure 4.1: **Rstudio AddIn Menu.** A screenshot of the `stmove` Report Builder add-in. This interactive menu guides users of the package within RStudio through the customization of their movement reports.

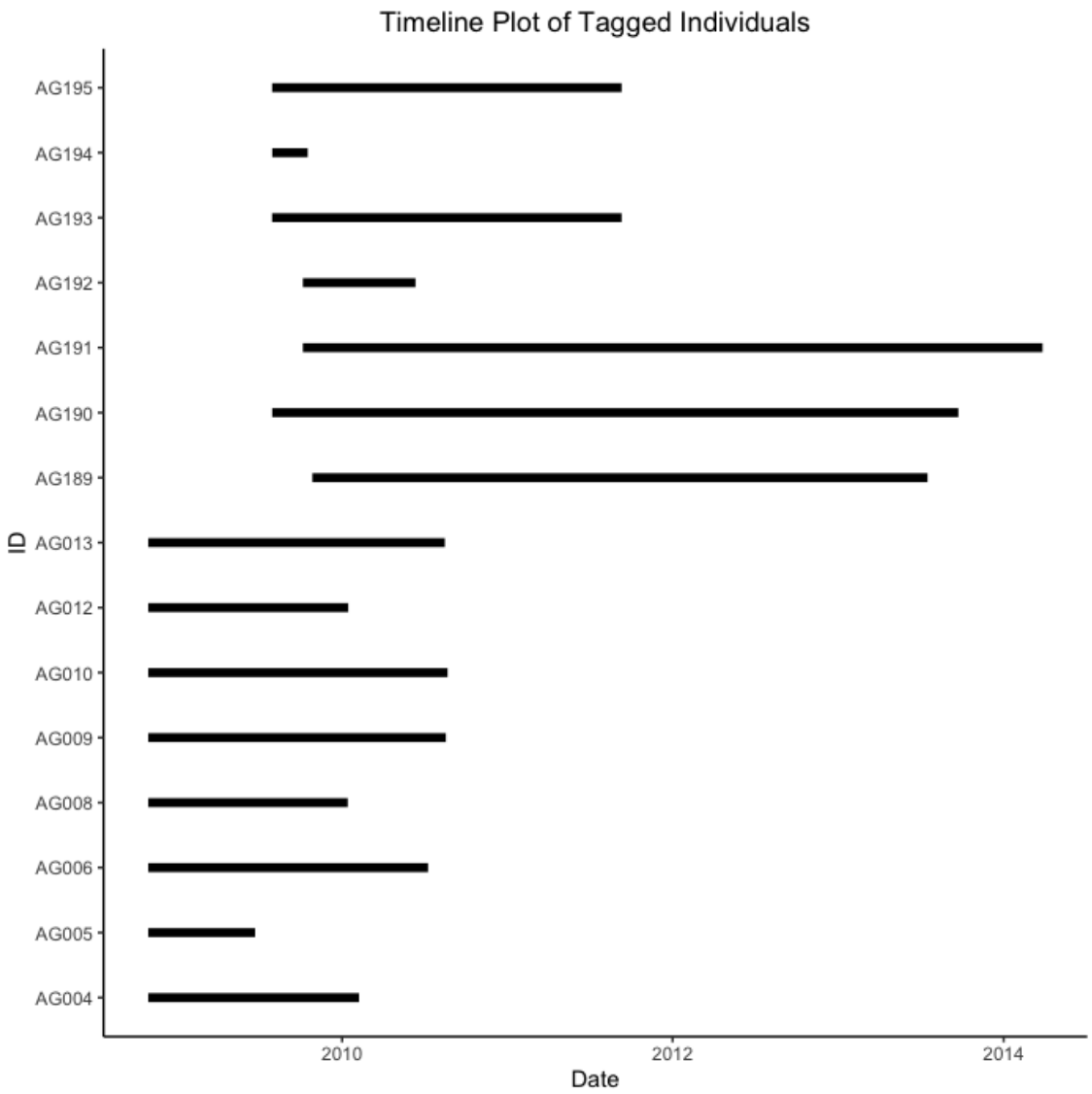

Figure 4.2: **Sampling Timeline Plot.** A segment graph demonstrating the sampling period for each individual in the elephant dataset. This is the output of `stmove`'s 'plot_timeline' function and is called by 'build_report' when given a data frame including multiple ids.

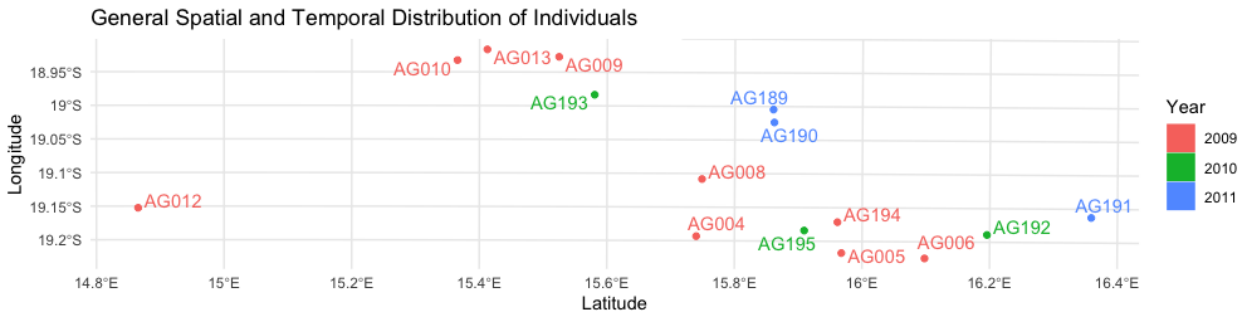

Figure 4.3: **Spatial Temporal Distribution Plot.** A map demonstrating the mean x and y locations of 15 individuals included in the elephant dataset.

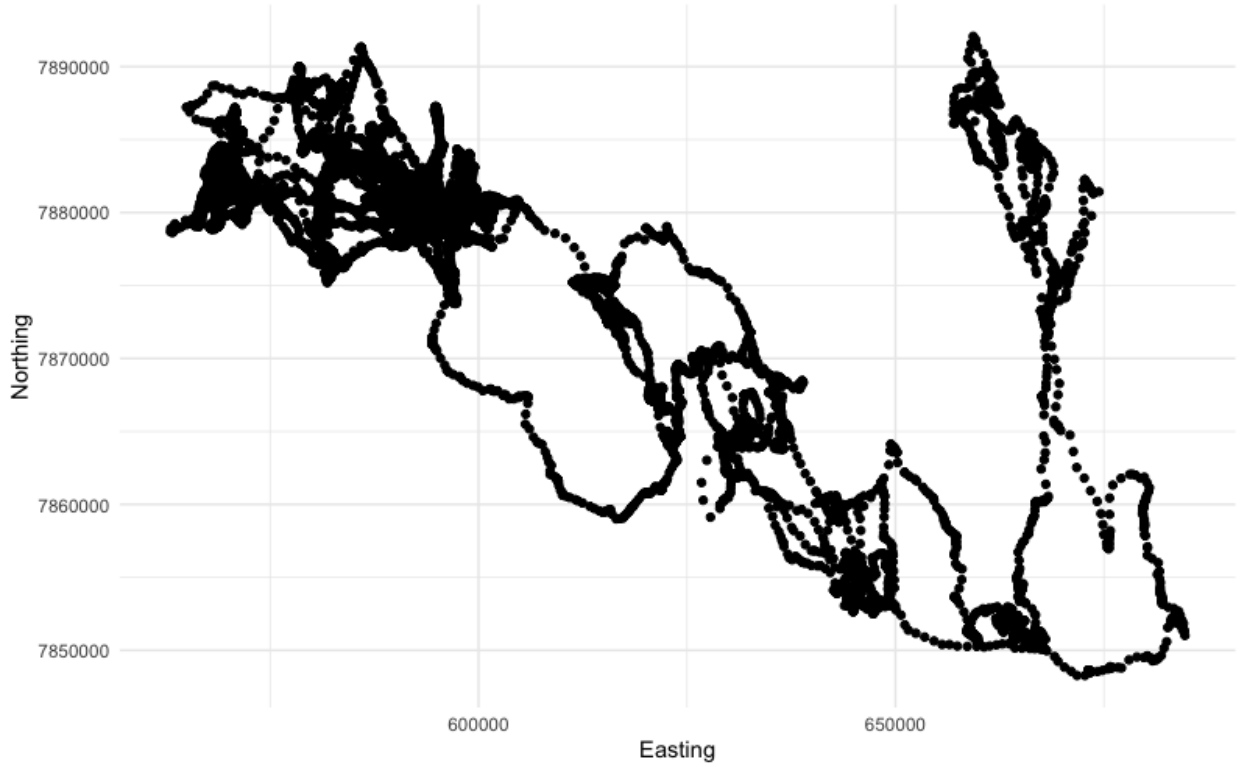

Figure 4.4: **Simple Coordinate Plot.** A simple x-y plot of coordinates along AG195's trajectory.

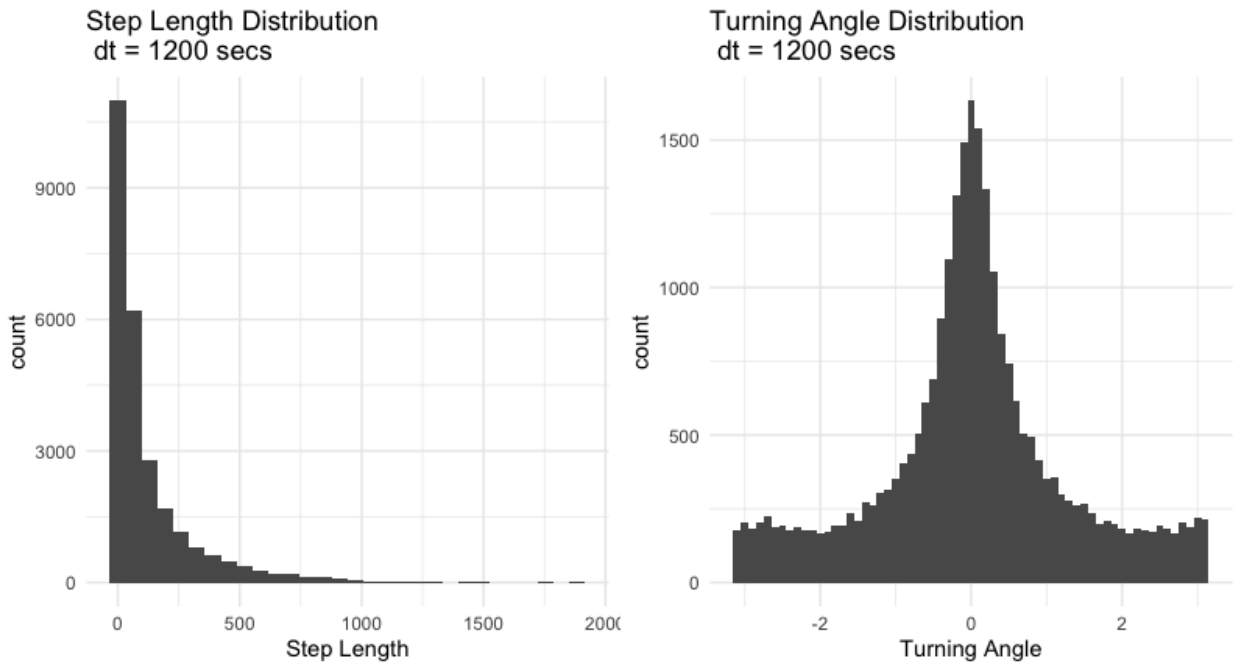

Figure 4.5: **Step Size and Turning Angle Distributions.** `stmove` reports include two histograms visualizing the distributions of primary movement metrics step size and relative turning angle.

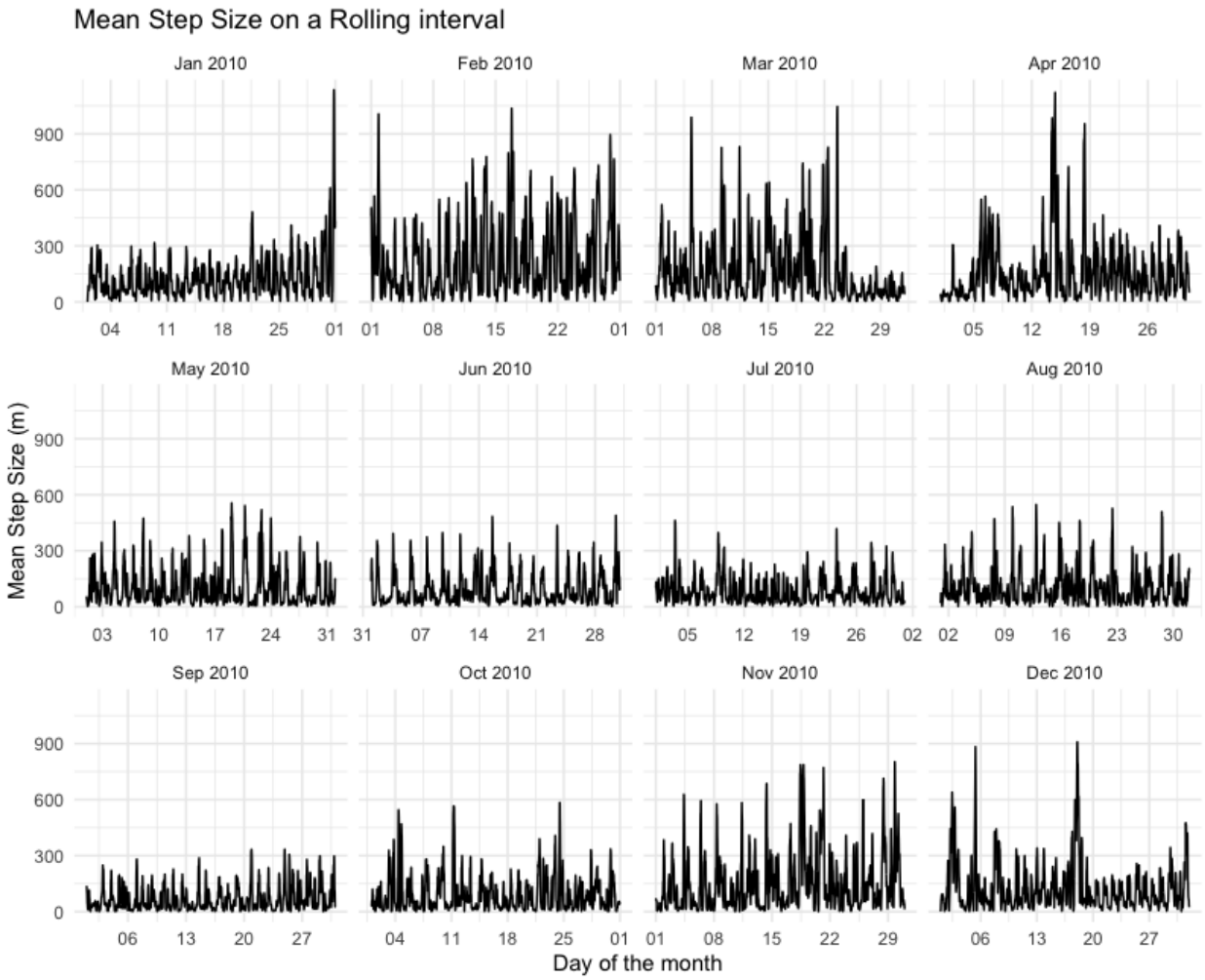

Figure 4.6: **Rolling Step Size.** A faceted plot of step size averaged using a rolling window of 3 hours using `stmove`'s 'rolling_stats' function. `stmove` reports include plots of rolling means for step length (s_t) and turning angle (θ_t), as well as rolling autocorrelations of both ($s_{t-1}s_t$ and $\theta_{t-1}\theta_t$) and a rolling cross-correlation between them ($s_t\theta_t$)

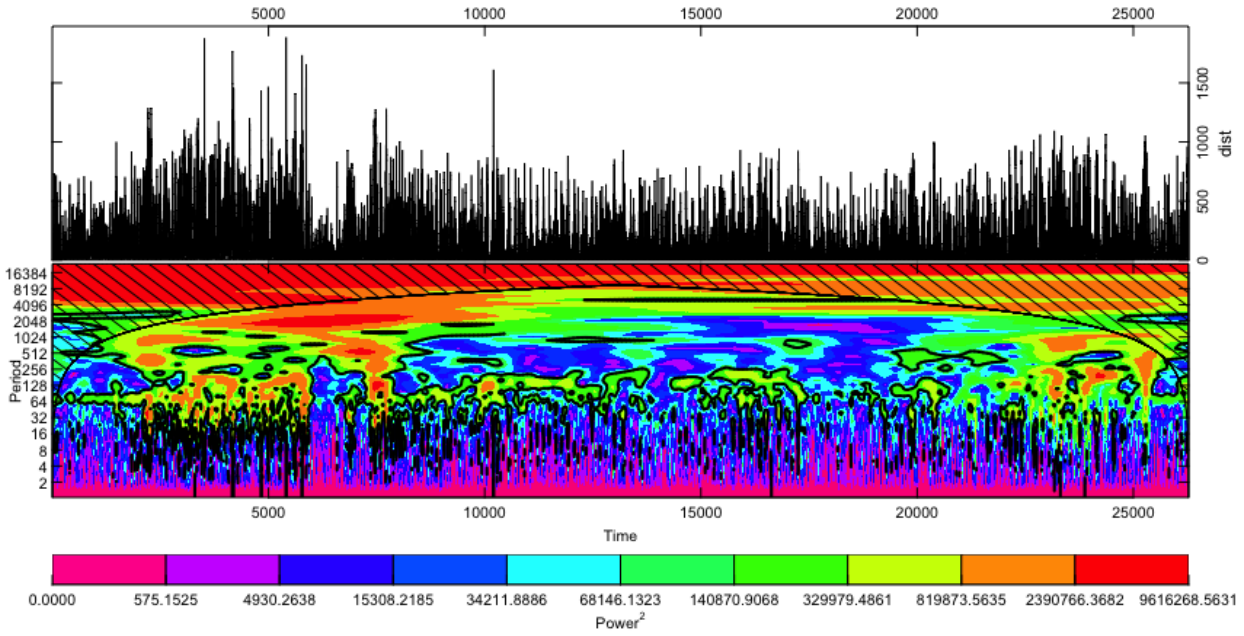

Figure 4.7: **Wavelet plot.** In the top half of the plot, the time series used for the wavelet analysis, in this case step length is plotted. In the lower plot, the power spectrum of the Morelet wavelet transform of this statistic is plotted. The lower left axis is the Fourier period corresponding to the wavelet scale of the top right axis. The bottom and top axes display time, represented simply as a time series index. Thus the units of all axes are subject to the underlying fix rate of the trajectory, in this case 20 minutes. The coloured $power^2$ contours are added for significance, the thick contour encloses regions of greater than 95% confidence. Cross-hatched regions on either end indicate the "cone of influence," where interpretation may be impacted by edge effects and should be avoided. These power spectrum plots are one way to investigate underlying periodicity in movement behavior from a trajectory's primary statistics.

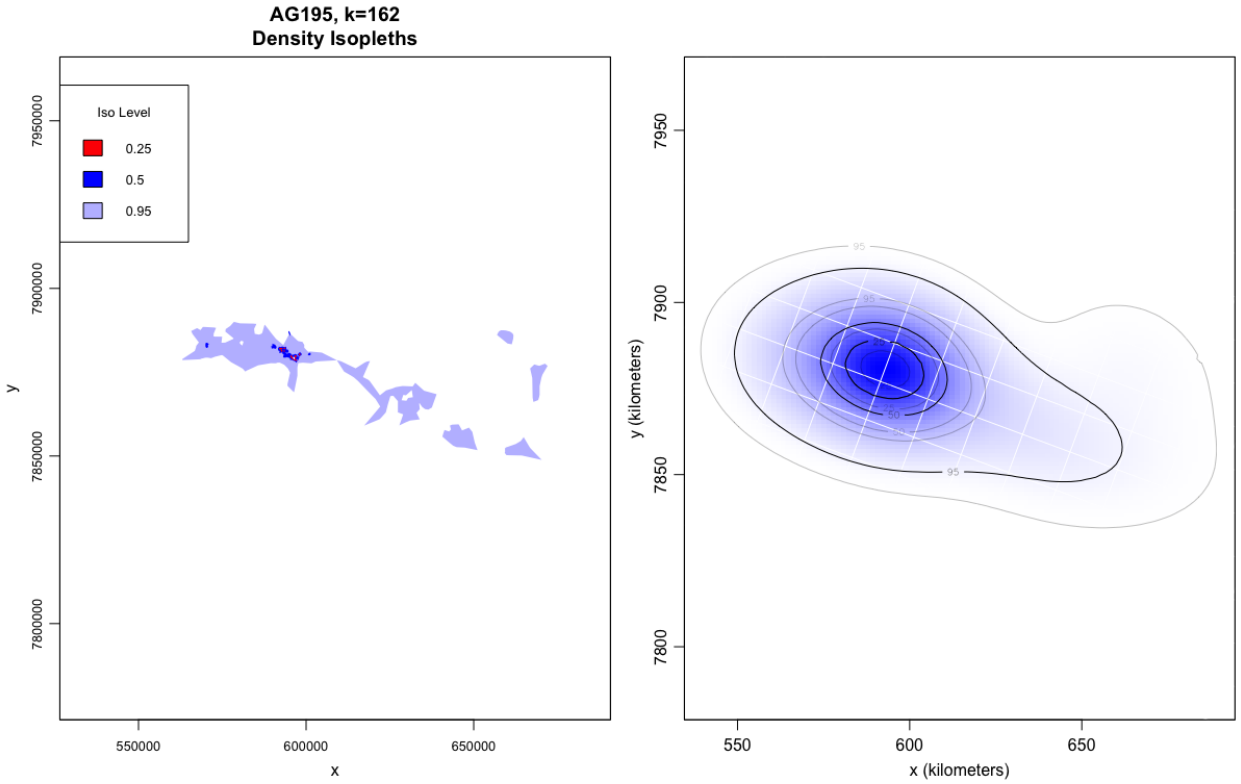

Figure 4.8: **Spatial Constructions.** A demonstration of `stmove`'s two spatial construction types, k-LoCoH and autocorrelated kernel density estimation. Note the difference in area estimation across the two non-parametric techniques.

Chapter 5

Conclusion

As tracking and computing technologies continue to advance, so will the development of novel metrics and methods in the sub-discipline of movement ecology. Our power to characterize animal space use and make inference and predictions regarding animal movement and behavior will only continue to advance. This increased ability to predict animal behavior and decisions, has implications for conservation, human-wildlife conflict, the spread of disease [52], and beyond. The chapters of this dissertation are presented as a review of the current state of movement analysis, an example of extending existing tools for use with irregular data, and a new package to better communicate and democratize movement ecology to those outside the field and/or new to tools of modern statistical computing.

This dissertation has focused primarily on methods and metrics used for understanding GPS relocation data. One of the most exciting areas of research in movement ecology not considered within these chapters is the application of complementary datasets [127] and recent advancement in statistical methods for prediction and classification of behavioral states, notably machine learning algorithms [20, 176, 23]. Also outside the scope of these chapters, but of interest to many movement ecologists, are advances in hierarchical and state space modelling [90], network analysis [40, 41, 136, 87], and methods for assessing dynamic interaction among conspecifics [110]. Though these are all without a doubt exciting, important areas of research within the discipline, my emphasis here on simple metrics applicable to a wide variety of data-sets was a conscious one; my goal to enhance the overall applicability of these tools to a larger audience. The work contained in this dissertation is meant to increase understanding, communication, and accessibility of movement ecology tools by managers and researchers writ large with the hope for real conservation impact and greater integration of movement analysis tools into science-based decision making. Movement data and the movement ecology discipline has an important role to play in predicting and understanding animal behavior, fitness, and range shifts, especially in the context of a changing climate.

Bibliography

[1] Briana Abrahms et al. "Does wildlife resource selection accurately inform corridor conservation?" In: *Journal of Applied Ecology* (2016).

[2] Briana Abrahms et al. "Suite of simple metrics reveals common movement syndromes across vertebrate taxa". In: *Movement ecology* 5.1 (2017), p. 12.

[3] B Abrahms et al. "Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads". In: *Animal Conservation* 19.3 (2016), pp. 247–255.

[4] F Adriaensen et al. "The application of 'least-cost' modelling as a functional landscape model". In: *Landscape and Urban Planning* 64.4 (2003), pp. 233–247.

[5] Sean C Ahearn and Somayeh Dodge. "Recursive multi-frequency segmentation of movement trajectories (ReMuS)". In: *Methods in Ecology and Evolution* 9.4 (2018), pp. 1075–1087.

[6] S.K. Alibhai and Z. Jewell. "Hot under the collar: the failure of radio-collars on black rhinoceros Diceros bicornis". en. In: *Oryx* 35 (2001), pp. 284–288.

[7] JJ Allaire et al. *rmarkdown: Dynamic Documents for R*. R package version 1.11. 2018. URL: `https://rmarkdown.rstudio.com`.

[8] Miguel B Araújo and A Townsend Peterson. "Uses and misuses of bioclimatic envelope modeling". In: *Ecology* 93.7 (2012), pp. 1527–1539.

[9] Vidya Athreya et al. "Translocation as a tool for mitigating conflict with leopards in human-dominated landscapes of India". In: *Conservation Biology* 25.1 (2011), pp. 133–141.

[10] Tal Avgar et al. "Integrated step selection analysis: bridging the gap between resource selection and animal movement". In: *Methods in Ecology and Evolution* 7.5 (2016), pp. 619–630.

[11] Shirli Bar-David et al. "Methods for assessing movement path recursion with application to African buffalo in South Africa". In: *Ecology* 90.9 (2009), pp. 2467–2479.

[12] Frédéric Barraquand and Simon Benhamou. "Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts". In: *Ecology* 89.12 (2008), pp. 3336–3348. ISSN: 1939-9170. DOI: 10.1890/08-0162.1. URL: http://dx.doi.org/10.1890/08-0162.1.

[13] Guillaume Bastille-Rousseau et al. "Flexible characterization of animal movement pattern using net squared displacement and a latent state model". In: *Movement Ecology* 4.1 (2016), p. 15.

[14] Douglas Bates et al. "Fitting Linear Mixed-Effects Models Using lme4". In: *Journal of Statistical Software* 67.1 (2015), pp. 1–48.

[15] Floris M van Beest and Jos M Milner. "Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate". In: *PLoS One* 8.6 (2013), e65972.

[16] Simon Benhamou. "How to reliably estimate the tortuosity of an animal's path:: straightness, sinuosity, or fractal dimension?" In: *Journal of theoretical biology* 229.2 (2004), pp. 209–220.

[17] Simon Benhamou and Louise Riotte-Lambert. "Beyond the Utilization Distribution: Identifying home range areas that are intensively exploited or repeatedly visited". In: *Ecological Modelling* 227 (2012), pp. 112–116.

[18] Oded Berger-Tal and Shirli Bar-David. "Recursive movement patterns: review and synthesis across species". In: *Ecosphere* 6.9 (2015), pp. 1–12.

[19] Miranda Bernard, Abraham Kielar, and Laura Booth. "The effects of mega-herbivore extinctions on seed dispersal and community structure in an East African Savanna". In: (2014).

[20] Owen R Bidder et al. "Love thy neighbour: automatic animal behavioural classification of acceleration data using the k-nearest neighbour algorithm". In: *PloS one* 9.2 (2014), e88609.

[21] Luca Börger and JM Fryxell. "Quantifying individual differences in dispersal using net squared displacement". In: *Dispersal ecology and evolution* (2012), pp. 222–230.

[22] Mark S Boyce and Lyman L McDonald. "Relating populations to habitats using resource selection functions". In: *Trends in Ecology & Evolution* 14.7 (1999), pp. 268–272.

[23] Ella Browning et al. "Predicting animal behaviour using deep learning: GPS data alone accurately predict diving in seabirds". In: *Methods in Ecology and Evolution* 9.3 (2018), pp. 681–692.

[24] Andrew G. Bunn. "A dendrochronology program library in R (dplR)". In: *Dendrochronologia* 26.2 (2008), pp. 115–124. ISSN: 1125-7865. DOI: 10.1016/j.dendro.2008.01.002.

[25] Andy Bunn et al. *dplR: Dendrochronology Program Library in R*. R package version 1.6.9. 2018. URL: `https://CRAN.R-project.org/package=dplR`.

[26] Nils Bunnefeld et al. "A model-driven approach to quantify migration patterns: individual, regional and yearly differences". In: *Journal of Animal Ecology* 80.2 (2011), pp. 466–476.

[27] Justin M Calabrese and William F Fagan. "A comparison-shopper's guide to connectivity metrics". In: *Frontiers in Ecology and the Environment* 2.10 (2004), pp. 529–536.

[28] Justin M Calabrese, Chris H Fleming, and Eliezer Gurarie. "ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process". In: *Methods in Ecology and Evolution* 7.9 (2016), pp. 1124–1132.

[29] Clément Calenge. "The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals". In: *Ecological modelling* 197.3-4 (2006), pp. 516–519.

[30] Clément Calenge, Stéphane Dray, and Manuela Royer-Carenzi. "The concept of animals' trajectories from a data analysis perspective". In: *Ecological Informatics* 4.1 (2009), pp. 34–41.

[31] Eric L Charnov. "Optimal foraging, the marginal value theorem". In: *Theoretical Population Biology* (2 1976).

[32] Cynthia Chen et al. "Evaluating the feasibility of a passive travel survey collection in a complex urban environment: Lessons learned from the New York City case study". In: *Transportation Research Part A: Policy and Practice* 44.10 (2010), pp. 830–840.

[33] Cynthia Chen et al. "The promises of big data and small data for travel behavior (aka human mobility) analysis". In: *Transportation research part C: emerging technologies* 68 (2016), pp. 285–299.

[34] Cheryl-Lesley B Chetkiewicz and Mark S Boyce. "Use of resource selection functions to identify conservation corridors". In: *Journal of Applied Ecology* 46.5 (2009), pp. 1036–1047.

[35] Justin G Clapp and Jeffrey L Beck. "Evaluating distributional shifts in home range estimates". In: *Ecology and Evolution* 5.18 (2015), pp. 3869–3878.

[36] EA Codling and NA Hill. "Sampling rate effects on measurements of correlated and biased random walks". In: *Journal of Theoretical Biology* 233.4 (2005), pp. 573–588.

[37] J Terry Coppock and David W Rhind. "The history of GIS". In: *Geographical information systems: Principles and applications*. Ed. by Michael F Goodchild, David W Rhind, and David J Maguire. London, UK: Longman scientific & technical, 1991, pp. 21–43.

[38] Tyler C Coverdale et al. "Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores". In: *Ecology* 97.11 (2016), pp. 3219–3230.

[39] Eric P Crist, Richard C Cicone, et al. "Application of the tasseled cap concept to simulated thematic mapper data". In: *Photogrammetric engineering and Remote sensing* 50.3 (1984), pp. 343–352.

[40] Darren P Croft, Richard James, and Jens Krause. *Exploring animal social networks*. Princeton University Press, 2008.

[41] Darren P Croft et al. "Hypothesis testing in animal social networks". In: *Trends in Ecology & Evolution* 26.10 (2011), pp. 502–507.

[42] Joris PGM Cromsigt and Dries PJ Kuijper. "Revisiting the browsing lawn concept: Evolutionary Interactions or pruning herbivores?" In: *Perspectives in Plant Ecology, Evolution and Systematics* 13.3 (2011), pp. 207–215.

[43] Graeme S Cumming and Daniel Cornélis. "Quantitative comparison and selection of home range metrics for telemetry data". In: *Diversity and Distributions* 18.11 (2012), pp. 1057–1065.

[44] Y De Beer and RJ Van Aarde. "Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas?" In: *Journal of Arid Environments* 72.11 (2008), pp. 2017–2025.

[45] María del Mar Delgado et al. "A statistical framework for inferring the influence of conspecifics on movement behaviour". In: *Methods in Ecology and Evolution* 5.2 (2014), pp. 183–189. ISSN: 2041-210X. DOI: 10.1111/2041-210X.12154. URL: http://dx.doi.org/10.1111/2041-210X.12154.

[46] Dydia DeLyser and Daniel Sui. "Crossing the qualitative-quantitative chasm III: Enduring methods, open geography, participatory research, and the fourth paradigm". In: *Progress in Human Geography* 38.2 (2014), pp. 294–307.

[47] Urška Demšar et al. "Stacked space-time densities: a geovisualisation approach to explore dynamics of space use over time". In: *GeoInformatica* 19.1 (2015), pp. 85–115.

[48] Eric Dinerstein et al. "An ecoregion-based approach to protecting half the terrestrial realm". In: *BioScience* 67.6 (2017), pp. 534–545.

[49] Somayeh Dodge, Robert Weibel, and Ehsan Forootan. "Revealing the physics of movement: Comparing the similarity of movement characteristics of different types of moving objects". In: *Computers, Environment and Urban Systems* 33.6 (2009), pp. 419–434.

[50] Somayeh Dodge et al. "Analysis of movement data". In: *International Journal of Geographical Information Science* 30.5 (2016), pp. 825–834.

[51] Eric R Dougherty et al. "A cross-validation-based approach for delimiting reliable home range estimates". In: *Movement ecology* 5.1 (2017), p. 19.

[52] Eric R. Dougherty et al. "Going through the motions: incorporating movement analyses into disease research". In: *Ecology Letters* (2018). ISSN: 1461-0248. DOI: 10.1111/ele.12917. URL: http://dx.doi.org/10.1111/ele.12917.

[53] Christopher E Doughty. "Herbivores increase the global availability of nutrients over millions of years". In: *Nature ecology & evolution* 1.12 (2017), p. 1820.

[54] Joni A Downs et al. "Voxel-based probabilistic space-time prisms for analysing animal movements and habitat use". In: *International Journal of Geographical Information Science* 28.5 (2014), pp. 875–890.

[55] Matthew R Dzialak et al. "Incorporating within-and between-patch resource selection in identification of critical habitat for brood-rearing greater sage-grouse". In: *Ecological Processes* 4.1 (2015), p. 5.

[56] Hendrik Edelhoff, Johannes Signer, and Niko Balkenhol. "Path segmentation for beginners: an overview of current methods for detecting changes in animal movement patterns". In: *Movement Ecology* 4.1 (2016), p. 21.

[57] Jane Elith, Michael Kearney, and Steven Phillips. "The art of modelling range-shifting species". In: *Methods in ecology and evolution* 1.4 (2010), pp. 330–342.

[58] William F Fagan and Justin M Calabrese. "Quantifying connectivity: balancing metric performance with data requirements". In: *Connectivity Conservation*. Ed. by Kevin R Crooks and M Sanjayan. Cambridge University Press, 2006.

[59] Per Fauchald and Torkild Tveraa. "Using First-Passage Time in the Analysis of Area-Restricted Search and Habitat Selection". In: *Ecology* 84.2 (2003), pp. 282–288.

[60] Gaelle Fehlmann et al. "Identification of behaviours from accelerometer data in a wild social primate". In: *Animal Biotelemetry* 5.1 (2017), p. 6.

[61] Sam M Ferreira et al. "Realization of poaching effects on rhinoceroses in Kruger National Park, South Africa". In: *African Journal of Wildlife Research* 48.1 (2018).

[62] John Fieberg and Luca Börger. "Could you please phrase "home range" as a question?" In: *Journal of Mammalogy* 93.4 (2012), pp. 890–902.

[63] John Fieberg and Christopher O Kochanny. "Quantifying home-range overlap: the importance of the utilization distribution". In: *Journal of Wildlife Management* 69.4 (2005), pp. 1346–1359.

[64] Christen H Fleming and Justin M Calabrese. "A new kernel density estimator for accurate home-range and species-range area estimation". In: *Methods in Ecology and Evolution* 8.5 (2017), pp. 571–579.

[65] DA Fornara and JT Du Toit. "Browsing lawns? Responses of Acacia nigrescens to ungulate browsing in an African savanna". In: *Ecology* 88.1 (2007), pp. 200–209.

[66] John A Gamon et al. “Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types”. In: *Ecological Applications* 5.1 (1995), pp. 28–41.

[67] Michael Garstang et al. “Response of African elephants (Loxodonta africana) to seasonal changes in rainfall”. In: *PLoS One* 9.10 (2014), e108736.

[68] Arild O Gautestad. “Brownian motion or Lévy walk? Stepping towards an extended statistical mechanics for animal locomotion”. In: *Journal of the Royal Society Interface* 9.74 (2012), pp. 2332–2340.

[69] Wayne M Getz and David Saltz. “A framework for generating and analyzing movement paths on ecological landscapes”. In: *Proceedings of the National Academy of Sciences* 105.49 (2008), pp. 19066–19071.

[70] Wayne M Getz and Christopher C Wilmers. “A local nearest-neighbor convex-hull construction of home ranges and utilization distributions”. In: *Ecography* 27.4 (2004), pp. 489–505.

[71] Wayne M Getz et al. “A web app for population viability and harvesting analyses”. In: *Natural Resource Modeling* 30.2 (2017), e12120.

[72] Wayne M Getz et al. “LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions”. In: *PLoS One* 2.2 (2007), e207.

[73] Wayne M Getz et al. “Panmictic and clonal evolution on a single patchy resource produces polymorphic foraging guilds”. In: *PloS one* 10.8 (2015), e0133732.

[74] Wayne M Getz et al. “Sympatric speciation in structureless environments”. In: *BMC evolutionary biology* 16.1 (2016), p. 50.

[75] Adrian C Gleiss, Rory P Wilson, and Emily LC Shepard. “Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure”. In: *Methods in Ecology and Evolution* 2.1 (2011), pp. 23–33.

[76] J. Goddard. “Home range, behaviour, and recruitment rates of two black rhinoceros populations”. en. In: *East African Wildlife Journal* 5 (1967), pp. 133–150.

[77] Marta C Gonzalez, Cesar A Hidalgo, and Albert-Laszlo Barabasi. “Understanding individual human mobility patterns”. In: *nature* 453.7196 (2008), p. 779.

[78] T. Gottert et al. “Habitat use and spatial organisation of relocated black rhinos in Namibia”. In: *Mammalia* 74 (2010), pp. 35–42.

[79] Eliezer Gurarie, Russel D Andrews, and Kristin L Laidre. “A novel method for identifying behavioural changes in animal movement data”. In: *Ecology Letters* 12.5 (2009), pp. 395–408.

[80] Eliezer Gurarie et al. “What is the animal doing? Tools for exploring behavioural structure in animal movements”. In: *Journal of Animal Ecology* 85.1 (2016), pp. 69–84.

[81] Ryan Gutenkunst et al. “Inferring resource distributions from Atlantic bluefin tuna movements: An analysis based on net displacement and length of track”. In: *Journal of Theoretical Biology* 245.2 (2007), pp. 243–257.

[82] R Dean Hardy and Mathew E Hauer. “Social vulnerability projections improve sea-level rise risk assessments”. In: *Applied Geography* 91 (2018), pp. 10–20.

[83] P.M. Hitchins. “Influence of vegetation types on sizes of home ranges of black rhinoceros, Hluhluwe Game Reserve, Zululand”. en. In: *Lammergeyer* 12 (1969), pp. 48–55.

[84] M. Hofmeyr. “Comparison of four different radio transmitter attachments on black rhino in Madikwe Game Reserve”. en. In: *Pachyderm* 26 (1998), pp. 14–24.

[85] Jon S Horne et al. “Analyzing animal movements using Brownian bridges”. In: *Ecology* 88.9 (2007), pp. 2354–2363.

[86] Philipp Hunziker. *velox: Fast Raster Manipulation and Extraction*. R package version 0.2.0. 2017. URL: `https://CRAN.R-project.org/package=velox`.

[87] David MP Jacoby and Robin Freeman. “Emerging network-based tools in movement ecology”. In: *Trends in Ecology & Evolution* 31.4 (2016), pp. 301–314.

[88] Z.C. Jewell, S.K. Alibhai, and P.R. Law. “Censusing and monitoring black rhino (*Diceros bicornis*) using an objective spoor (Footprint) identification technique”. In: *Journal of Zoology* 254 (2001), pp. 1–16.

[89] Kate E Jones et al. “Global trends in emerging infectious diseases”. In: *Nature* 451.7181 (2008), pp. 990–993.

[90] Ian D Jonsen, Joanna Mills Flemming, and Ransom A Myers. “Robust state–space modeling of animal movement data”. In: *Ecology* 86.11 (2005), pp. 2874–2880.

[91] Knud Andreas Jønsson et al. “Tracking animal dispersal: from individual movement to community assembly and global range dynamics”. In: *Trends in ecology & evolution* 31.3 (2016), pp. 204–214.

[92] Rocio Joo et al. “Navigating through the R packages for movement”. In: *arXiv preprint arXiv:1901.05935* (2019).

[93] Roland Kays et al. “Terrestrial animal tracking as an eye on life and planet”. In: *Science* 348.6240 (2015), aaa2478.

[94] Rob Kitchin. “Big data and human geography: Opportunities, challenges and risks”. In: *Dialogues in human geography* 3.3 (2013), pp. 262–267.

[95] Martin Kulldorff et al. “Evaluating cluster alarms: a space-time scan statistic and brain cancer in Los Alamos, New Mexico”. In: *American journal of public health* 88.9 (1998), pp. 1377–1380.

[96] Shawn W Laffan, Andrew K Skidmore, and Janet Franklin. “Geospatial analysis of species, biodiversity and landscapes: introduction to the second special issue on spatial ecology”. In: *International journal of geographical information science* 26.11 (2012), pp. 2003–2007.

[97] Shawn William Laffan, Andrew K Skidmore, and Janet Franklin. "Space, time, connectivity and conflict in biological landscapes: the fourth special issue on spatial ecology". In: *International journal of geographical information science* 30.1 (2016), pp. 1–4.

[98] Shawn William Laffan, Andrew K Skidmore, and Janet Franklin. "Species distribution and diversity, habitat selection and connectivity: introduction to the Third Special Issue on Spatial Ecology". In: *International Journal of Geographical Information Science* 28.8 (2014), pp. 1527–1530.

[99] Patrick Laube and Ross S Purves. "How fast is a cow? cross-scale analysis of movement data". In: *Transactions in GIS* 15.3 (2011), pp. 401–418.

[100] P.R. Law, Z. Jewell, and S. Alibhai. "Using Shape and Size to Quantify Variation in Footprints for Individual Identification: Case Study With White Rhinoceros *(Ceratotherium simum)*". en. In: *Wildlife Society Bulletin* 37 (2013), pp. 433–438.

[101] Emmanuel Lazaridis. *lunar: Lunar Phase & Distance, Seasons and Other Environmental Factors*. (Version 0.1-04). 2014. URL: `http://statistics.lazaridis.eu`.

[102] Subhash R Lele et al. "Selection, use, choice and occupancy: clarifying concepts in resource selection studies". In: *Journal of Animal Ecology* 82.6 (2013), pp. 1183–1191.

[103] R. van Lieverloo et al. "A comparison of faecal analysis with backtracking to determine the diet composition and species preference of the black rhinoceros (*Diceros bicornis minor*)". en. In: *European Journal of Wildlife Research* 55 (2009), pp. 505–515.

[104] W. Linklater. "Science and management in a conservation crisis: a case study with rhinoceros". In: *Conservation Biology* 17 (2003), pp. 968–976.

[105] W. Linklater and I. Hutcheson. "Black rhinoceros are slow to colonize a harvested neighbour's range". en. In: *South African Journal of Wildlife Research* 40 (2010), pp. 58–63.

[106] W. Linklater and A. Shrader. "Rhino management challenges: spatial and social ecology for habitat and population management". en. In: *Conserving Africa's Mega-Diversity in the Anthropocene*. Ed. by Joris P.G.M. Cromsigt, Sally Archibald, and Norman Owen-Smith. Cambridge, UK: Cambridge University Press, 2017, pp. 265–285.

[107] W. Linklater and R. Swaisgood. "Reserve size, release density and translocation success: Black rhinoceros movements, association, injury and death after release". en. In: *Journal of Wildlife Management* 72 (2008), pp. 1059–1068.

[108] Jed Long. "A Field-Based Time Geography for Wildlife Movement Analysis". In: *International Conference on GIScience Short Paper Proceedings*. Vol. 1. 1. 2016.

[109] Jed A Long and Trisalyn A Nelson. "A review of quantitative methods for movement data". In: *International Journal of Geographical Information Science* 27.2 (2013), pp. 292–318.

[110] Jed A Long and Trisalyn A Nelson. "Measuring dynamic interaction in movement data". In: *Transactions in GIS* 17.1 (2013), pp. 62–77.

[111] Jed A Long et al. "A critical examination of indices of dynamic interaction for wildlife telemetry studies". In: *Journal of Animal Ecology* 83.5 (2014), pp. 1216–1233.

[112] Andrew J Lyons, Wendy C Turner, and Wayne M Getz. "Home range plus: a space-time characterization of movement over real landscapes". In: *Movement Ecology* 1.1 (2013), p. 2.

[113] Andrew Lyons and Wayne Getz. *T-LoCoH: Time Local Convex Hull Homerange and Time Use Analysis*. R package version 1.40.05. 2018. URL: https://R-Forge.R-project.org/projects/tlocoh/.

[114] Andy Lyons. *tlocoh.dev: Development package for tlocoh*. R package version 1.34.00/r12. 2018. URL: https://R-Forge.R-project.org/projects/tlocoh-dev/.

[115] Shimane W Makhabu and Christina Skarpe. "Rebrowsing by elephants three years after simulated browsing on five woody plant species in northern Botswana". In: *South African Journal of Wildlife Research* 36.1 (2006), pp. 99–102.

[116] BFL Manly et al. *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media, 2007.

[117] Hannah W McKenzie, Mark A Lewis, and Evelyn H Merrill. "First passage time analysis of animal movement and insights into the functional response". In: *Bulletin of mathematical biology* 71.1 (2009), pp. 107–129.

[118] JS McManus et al. "Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms". In: *Oryx* 49.4 (2015), pp. 687–695.

[119] Brad H McRae et al. "Using circuit theory to model connectivity in ecology, evolution, and conservation". In: *Ecology* 89.10 (2008), pp. 2712–2724.

[120] Theo Michelot, Roland Langrock, and Toby A. Patterson. "moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models". In: *Methods in Ecology and Evolution* 7.11 (2016), pp. 1308–1315. DOI: 10.1111/2041-210X.12578.

[121] Joshua J Millspaugh et al. "Comparability of three analytical techniques to assess joint space use". In: *Wildlife Society Bulletin* 32.1 (2004), pp. 148–157.

[122] A Mondanaro et al. "Living with the elephant in the room: top-down control in Eurasian large mammal diversity over the last 22 million years". In: *Palaeogeography, palaeoclimatology, palaeoecology* 485 (2017), pp. 956–962.

[123] Juan Manuel Morales et al. “Extracting more out of relocation data: building movement models as mixtures of random walks”. In: *Ecology* 85.9 (2004), pp. 2436–2445.

[124] Steffen Moritz and Thomas Bartz-Beielstein. “imputeTS: Time Series Missing Value Imputation in R”. In: *The R Journal* 9.1 (2017), pp. 207–218. URL: https://journal.r-project.org/archive/2017/RJ-2017-009/index.html.

[125] Giorgos Mountrakis and Kari Gunson. “Multi-scale spatiotemporal analyses of moose–vehicle collisions: a case study in northern Vermont”. In: *International Journal of Geographical Information Science* 23.11 (2009), pp. 1389–1412.

[126] Ran Nathan et al. “A movement ecology paradigm for unifying organismal movement research”. In: *Proceedings of the National Academy of Sciences* 105.49 (2008), pp. 19052–19059.

[127] Ran Nathan et al. “Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures”. In: *Journal of Experimental Biology* 215.6 (2012), pp. 986–996.

[128] Michael J Noonan et al. “A comprehensive analysis of autocorrelation and bias in home range estimation”. In: *Ecological Monographs* 89.2 (2019), e01344.

[129] Morten Odden et al. “Adaptable neighbours: movement patterns of GPS-collared leopards in human dominated landscapes in India”. In: *PLoS One* 9.11 (2014), e112044.

[130] T.W. Oloo, R. Brett, and T.P. Young. “Seasonal variation in the feeding ecology of black rhinoceros (*Diceros bicornis L.*) in Laikipia”. en. In: *Kenya. African Journal of Ecology* 32 (1994), pp. 142–157.

[131] R. Norman Owen-Smith. *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge Studies in Ecology. Cambridge: Cambridge University Press, 1988.

[132] Toby A Patterson et al. “Classifying movement behaviour in relation to environmental conditions using hidden Markov models”. In: *Journal of Animal Ecology* 78.6 (2009), pp. 1113–1123.

[133] Toby A Patterson et al. “State–space models of individual animal movement”. In: *Trends in ecology & evolution* 23.2 (2008), pp. 87–94.

[134] Edzer Pebesma. “Simple Features for R: Standardized Support for Spatial Vector Data”. In: *The R Journal* (2018). URL: https://journal.r-project.org/archive/2018/RJ-2018-009/index.html.

[135] Elizabeth Pennisi. “Global tracking of small animals gains momentum”. In: *Science* 334 (2011).

[136] Noa Pinter-Wollman et al. “The dynamics of animal social networks: analytical, conceptual, and theoretical advances”. In: *Behavioral Ecology* (2013), art047.

[137] R. Plotz and W. Linklater. "Black rhinoceros (*Diceros bicornis: Rhinocerotidae*) calf succumbs after lion predation attempt: implications for conservation management". en. In: *African Zoology* 42 (2009), pp. 283–287.

[138] R.D. Plotz et al. "Standardising Home Range Studies for Improved Management of the Critically Endangered Black Rhinoceros". en. In: *Plos One* 11 (2016).

[139] Leo Polansky, Werner Kilian, and George Wittemyer. "Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state–space models". In: *Proceedings of the Royal Society B: Biological Sciences* 282.1805 (2015), p. 20143042.

[140] Leo Polansky et al. "From moonlight to movement and synchronized randomness: Fourier and wavelet analyses of animal location time series data". In: *Ecology* 91.5 (2010), pp. 1506–1518. ISSN: 1939-9170. DOI: 10.1890/08-2159.1. URL: http://dx.doi.org/10.1890/08-2159.1.

[141] Roger A Powell and Michael S Mitchell. "What is a home range?" In: *Journal of Mammalogy* 93.4 (2012), pp. 948–958.

[142] Lama Qasem et al. "Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector?" In: *PloS one* 7.2 (2012), e31187.

[143] R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria, 2018. URL: https://www.R-project.org/.

[144] Melissa R Rice, Beth A Middleton, and David J Gibson. "Fractal analysis of movement pathways of earthworms in vegetated and unvegetated landscapes". In: *Bios* (1998), pp. 176–184.

[145] Stephen H Roxburgh, Katriona Shea, and J Bastow Wilson. "The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence". In: *Ecology* 85.2 (2004), pp. 359–371.

[146] J Andrew Royle et al. "Spatial capture–recapture models for jointly estimating population density and landscape connectivity". In: *Ecology* 94.2 (2013), pp. 287–294.

[147] Sarah C Sawyer, Clinton W Epps, and Justin S Brashares. "Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes?" In: *Journal of Applied Ecology* 48.3 (2011), pp. 668–678.

[148] R. Schenkel and L. Schenkel-Hulliger. *Ecology and behaviour of the black rhinoceros (Diceros bicornis L.): A field study*. en. Harvey, Hamburg and Berlin, Germany: Verlag Paul, 1969.

[149] Dana P Seidel and Mark S Boyce. "Patch-use dynamics by a large herbivore". In: *Movement Ecology* 3.1 (2015), p. 7.

[150] Dana Paige Seidel, Eric R Dougherty, and Wayne M Getz. "Exploratory movement analysis and report building R package `stmove`". In: (). In Prep.

[151] Dana Paige Seidel et al. "Ecological metrics and methods for GPS movement data". In: *International Journal of Geographical Information Science* 32.11 (2018), pp. 2272–2293.

[152] Emily LC Shepard et al. "Identification of animal movement patterns using tri-axial accelerometry". In: *Endangered Species Research* 10 (2008), pp. 47–60.

[153] A. Shrader and B. Beauchamp. "A new method for implanting radio transmitters into the horns of black and white rhinoceros". en. In: *Pachyderm* 30 (2001), pp. 81–86.

[154] MJ Silk et al. "Using social network metrics in wildlife disease ecology, epidemiology and management". In: *BioScience* 67.3 (2017), pp. 245–257.

[155] Andrew K Skidmore et al. "Geospatial tools address emerging issues in spatial ecology: a review and commentary on the Special Issue". In: *International Journal of Geographical Information Science* 25.3 (2011), pp. 337–365.

[156] R. Slotow and G. van Dyk. "Role of delinquent young örphanmale elephants in high mortality of white rhinoceros in Pilanesberg National Park". en. In: *Koedoe* 44 (2001), pp. 85–94.

[157] Peter E Smouse et al. "Stochastic modelling of animal movement". In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1550 (2010), pp. 2201–2211.

[158] Chaoming Song et al. "Limits of predictability in human mobility". In: *Science* 327.5968 (2010), pp. 1018–1021.

[159] Chaoming Song et al. "Modelling the scaling properties of human mobility". In: *Nature Physics* 6.10 (2010), p. 818.

[160] David W Stephens and John R Krebs. *Foraging theory*. Princeton University Press, 1986.

[161] Daniel Sui. "Opportunities and impediments for open GIS". In: *Transactions in GIS* 18.1 (2014), pp. 1–24.

[162] Maitreyi Sur et al. "Change detection in animal movement using discrete wavelet analysis". In: *Ecological Informatics* 20 (2014), pp. 47–57.

[163] Craig J Tambling et al. "Methods for locating African lion kills using global positioning system movement data". In: *Journal of Wildlife Management* 74.3 (2010), pp. 549–556.

[164] Henrik Thurfjell, Simone Ciuti, and Mark S Boyce. "Applications of step-selection functions in ecology and conservation". In: *Movement Ecology* 2.1 (2014), p. 4.

[165] Lutz Tischendorf and Lenore Fahrig. "On the usage and measurement of landscape connectivity". In: *Oikos* 90.1 (2000), pp. 7–19.

[166] Stella W Todd and Roger M Hoffer. "Responses of spectral indices to variations in vegetation cover and soil background". In: *Photogrammetric engineering and remote sensing* 64 (1998), pp. 915–922.

[167] R. du Toit. "Rationale for ongoing radio-collaring of black rhinos - a response to Alibhai and Jewell". en. In: *Oryx* 35 (2001), pp. 289–290.

[168] Stanley M Tomkiewicz et al. "Global positioning system and associated technologies in animal behaviour and ecological research". In: *Philosophical Transactions of the Royal Society B* 365.1550 (2010), pp. 2163–2176.

[169] Christopher Torrence and Gilbert P. Compo. "A Practical Guide to Wavelet Analysis". In: *Bulletin of the American Meteorological Society* 79.1 (1998), pp. 61–78.

[170] Christopher H Trisos et al. "Potentially dangerous consequences for biodiversity of solar geoengineering implementation and termination". In: *Nature Ecology e& Evolution* (2018), p. 1.

[171] Miriam Tsalyuk et al. "Temporal variation in resource selection of African elephants follows long-term variability in resource availability". In: *Ecological Monographs* (2019), e01348.

[172] Peter Turchin. *Quantitative analysis of movement*. Sinauer Associates, Inc.), 1998.

[173] Wendy C Turner et al. "Soil ingestion, nutrition and the seasonality of anthrax in herbivores of Etosha National Park". In: *Ecosphere* 4.1 (2013), pp. 1–19.

[174] Joshua Ulrich. *TTR: Technical Trading Rules*. R package version 0.23-4. 2018. URL: https://CRAN.R-project.org/package=TTR.

[175] Kevin Ushey. *RcppRoll: Efficient Rolling / Windowed Operations*. R package version 0.3.0. 2018. URL: https://CRAN.R-project.org/package=RcppRoll.

[176] John Joseph Valletta et al. "Applications of machine learning in animal behaviour studies". In: *Animal Behaviour* 124 (2017), pp. 203–220.

[177] Bram Van Moorter et al. "Identifying movement states from location data using cluster analysis". In: *Journal of Wildlife Management* 74.3 (2010), pp. 588–594.

[178] Bram Van Moorter et al. "Memory keeps you at home: a mechanistic model for home range emergence". In: *Oikos* 118.5 (2009), pp. 641–652.

[179] Bram Van Moorter et al. "Movement is the glue connecting home ranges and habitat selection". In: *Journal of Animal Ecology* 85.1 (2016), pp. 21–31.

[180] Webster Van Winkle. "Comparison of several probabilistic home-range models". In: *Journal of Wildlife Management* (1975), pp. 118–123.

[181] Eric Vander Wal and AR Rodgers. "An individual-based quantitative approach for delineating core areas of animal space use". In: *Ecological Modelling* 224.1 (2012), pp. 48–53.

[182] Matthew S Waldram, William J Bond, and William D Stock. "Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna". In: *Ecosystems* 11.1 (2008), pp. 101–112.

[183] Richard Walker and Lance Craighead. "Analyzing wildlife movement corridors in Montana using GIS". In: *Proceedings of the 1997 ESRI user conference*. (Redlands, CA). 1997.

[184] Yiwei Wang et al. "Movement, resting, and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements". In: *Movement ecology* 3.1 (2015), p. 2.

[185] Nathan F. Webb, Mark Hebblewhite, and Evelyn H. Merrill. "Statistical methods for identifying wolf kill sites using Global Positioning System locations". In: *Journal of Wildlife Management* 72.3 (2008), pp. 798–807. ISSN: 1937-2817. DOI: 10.2193/2006-566. URL: http://dx.doi.org/10.2193/2006-566.

[186] John Weier and David Herring. "Measuring vegetation (NDVI & EVI)". In: *NASA Earth Observatory* 20 (2000).

[187] A.M. White, R.R. Swaisgood, and N. Czekala. "Ranging patterns in white rhinoceros, *Ceratotherium simum simum*: implications for mating strategies". en. In: *Animal Behaviour* 74 (2007), pp. 349–356.

[188] Hadley Wickham. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag, 2016. ISBN: 978-3-319-24277-4. URL: https://ggplot2.tidyverse.org.

[189] M. Wikelski and R. Kays. "Movebank: archive, analysis and sharing of animal movement data". In: (2018). Hosted by the Max Planck Institute for Ornithology. www.movebank.org, accessed on 05-01-2018.

[190] Rory P Wilson, ELC Shepard, and N Liebsch. "Prying into the intimate details of animal lives: use of a daily diary on animals". In: *Endangered Species Research* 4.1-2 (2008), pp. 123–137.

[191] George Wittemyer et al. "Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses". In: *Proceedings of the National Academy of Sciences* 105.49 (2008), pp. 19108–19113.

[192] Rosie Woodroffe et al. "Effects of culling on badger Meles meles spatial organization: implications for the control of bovine tuberculosis". In: *Journal of Applied Ecology* 43.1 (2006), pp. 1–10.

[193] BJ Worton. "A review of models of home range for animal movement". In: *Ecological modelling* 38.3-4 (1987), pp. 277–298.

[194] Brian J Worton. "Kernel methods for estimating the utilization distribution in home-range studies". In: *Ecology* 70.1 (1989), pp. 164–168.

[195] Yihui Xie, J.J. Allaire, and Garrett Grolemund. *R Markdown: The Definitive Guide*. ISBN 9781138359338. Boca Raton, Florida: Chapman and Hall/CRC, 2018. URL: https://bookdown.org/yihui/rmarkdown.

[196] May Yuan. "30 years of IJGIS: the changing landscape of geographical information science and the road ahead". In: *International Journal of Geographical Information Science* 31.3 (2017), pp. 425–434.

[197] Katherine A Zeller, Kevin McGarigal, and Andrew R Whiteley. "Estimating landscape resistance to movement: a review". In: *Landscape Ecology* 27.6 (2012), pp. 777–797.

[198] Katherine A Zeller et al. "Using step and path selection functions for estimating resistance to movement: pumas as a case study". In: *Landscape Ecology* 31.6 (2016), pp. 1319–1335.

[199] Royi Zidon et al. "Zebra migration strategies and anthrax in Etosha National Park, Namibia". In: *Ecosphere* 8.8 (2017).